

Thesis/
Reports
Hatch,
C. R.

Studies on Western Spruce Budworm
Population Dynamics

FINAL REPORT

STUDIES ON WESTERN SPRUCE BUDWORM POPULATION DYNAMICS

- 1983 -

Principal Investigator: Charles Hatch
College of Forestry, Wildlife, and Range Sciences
University of Idaho
Moscow, Idaho 83843

Lead Scientist: J. J. Colbert
CANUSA-W Budworms Program
Pacific Northwest Experiment Station
Portland, Oregon 97208

Investigating Scientists: Torolf R. Torgersen and Robert W. Campbell

Organizations: Forestry and Range Sciences Laboratory
LaGrande, Oregon 97850
and
New York State College of Environmental
Sciences and Forestry
Syracuse, New York 13210

Accepted
J. J. Colbert
8/11/86

Introduction

During the period between 1979 and 1983, we entered into a series of cooperative agreements with CANUSA-West. Through these agreements we have been funded to examine a broad range of attributes of western spruce budworm populations. In each population we studied in Washington, Oregon, Idaho, and Montana, we collected detailed mortality and density information on the sequence of intrageneration life stages. We also obtained detailed information on the role of predaceous birds and ants, and on the parasitoid complex at all the study sites.

With the above information as a background, we have synthesized a conceptual model of budworm dynamics. The final development of that model will be covered under a separate negotiated Cooperative Agreement PNW-84-388. In the course of our previous studies several opportunities for promising lines of research emerged. In addition, the approval for an operational carbaryl treatment of portions of the Malheur National Forest infested with spruce budworm presented other opportunities. Given the data base we had to date, and in the light of the planned carbaryl treatment, we characterized the objectives of this years investigations and tasks as follows: 1, to determine the effects of the John Day area carbaryl treatment on predaceous woodland ants; 2, to characterize the habitat requirements of foliage-foraging woodland ants in northeastern Oregon and northwestern Montana; 3, to complete dissections of parasitized budworm material and measure budworm head capsules, and execute data entry to permit further analysis; and 4, to summarize, analyse, and synthesize remaining population data into textual form for relevant program-ending documents. The latter presumes that these data and conclusions will be made available to the modeling effort of Colbert, Sheehan, Crookston, and Kemp, and will reside in RWU-2201, now located at the Forestry and Range Sciences Laboratory, LaGrande.

Results

Each of the stated objectives was, in effect, the subject of an independent study. The accompanying reports and published manuscripts are submitted as fulfillment of objectives 1 and 2 dealing with foliage-foraging predaceous woodland ants; Appendix documents I, II, III, and IV.

Information derived from the dissection of parasitized host budworm material collected from study sites in Washington, Oregon, Montana, and Idaho, objective 3 in part, is reported in a manuscript on the role of parasites in budworm dynamics; Appendix V. The data are stored and appropriately backed up in the Data General MV-4000 at the Forestry and Range Sciences Laboratory, LaGrande. The remaining material relating to budworm head capsule distributions is also stored in the above system; Appendix VI.

Correspondence, Appendix VIIa-g, and manuscript in press, Appendix VIII, document compliance with objective 4. The manuscript in press will be published as Campbell, R.W. 1986. Population Dynamics. Chapter 6. In Western Spruce Budworm. M.H. Brookes, R.W. Campbell, J.J. Colbert, R.G. Mitchell, and R.W. Stark eds. USDA Tech. Bull. 1649.

Work Remaining on the Study

In some ways the work connected with, or deriving from the studies reported herein will not have a specific end. The reports, published material, and data will continue to feed scholarly endeavors to understand the budworm life system for many years into the future. Currently, work is underway to fine-tune both a synoptic and a detailed model describing budworm dynamics. Analyses are in progress to characterize the structure of budworm larval instar distributions in relation to seasonal development and to outbreak dynamics. Life table data and larval sampling data continue to be used to supplement sampling validation efforts.

Cooperation and Coordination

A great many administrative entities have been involved directly or perpherally in the execution of this Cooperative Agreement. We acknowledge the help and cooperation of Region 6 Forest Insect and Disease Management Entomologists; Norman Cimon, Systems Analyst, and personnel on the Bear Valley Ranger District, Malheur National Forest; Kevin P. Hosman, Research Associate, University of Idaho, School of Forestry, Wildlife, and Range Sciences; and Fred H. Schmidt, Biological Technician, Forestry and Range Sciences Laboratory. We are indebted to Janet Gilliland, formerly PNW Office of Fiscal Management and Budget, for her cheerful and long-suffering help in expediting this and related cooperative agreements and numerous amendments over a five-year period - to her this report is dedicated. Also, we acknowledge the patient attention to our personnel and administrative needs by the staff of Budget and Fiscal Management, School of Forestry, Wildlife, and Range Management, University of Idaho - especially Kathy Rummelhart, Richard Bottger, Lynn Kittner, and Linda Odenborg.

Appendix

- I - Effects of an aerial carbaryl treatment on woodland ants, by Christopher F. Murphy.
- II - Habitat requirements of foliage-foraging predaceous woodland ants in eastern Oregon and western Montana, by Lorna C. Youngs and Robert W. Campbell.
- III - Predaceous ants in biological control of insect pests of North American forests, by Lorna C. Youngs.
- IV - Ants preying on pupae of the western spruce budworm, Choristoneura occidentalis (Lepidoptera:Tortricidae), in eastern Oregon and western Montana, by Lorna C. Youngs.
- V - Role of parasites in the population dynamics of the western spruce budworm (Lepidoptera:Tortricidae) in the Northwest, by Torolf R. Torgersen, Robert W. Campbell, Nilima Srivastava, and Roy C. Beckwith.
- VI - Documentation of laval head capsule measurements, Data General MV - 4000, Forestry and Range Sciences Laboratory, LaGrande, Oregon 97850.
- VII - Correspondence documenting receipt, analysis, and storage of study results.
- VIII - Western Spruce Budworm - Introduction, by Robert W. Campbell. Manuscript in press, In Western Spruce Budworm. USDA Tech. Bull. 1694. 1986. eds. Brookes, Campbell, Colbert, Mitchell, and Stark.

Appendix I

**Effects of an Aerial Carbaryl Treatment
on Woodland Ants**

by

**Christopher F. Murphy
Department of Entomology
Oregon State University
Corvallis, Oregon**

**Principal Investigator
George Belt, University of Idaho, Moscow, Idaho**

**Lead Scientist
Torolf R. Torgersen, Forestry and Range Sciences
Laboratory, LaGrande, Oregon**

INTRODUCTION

Efficient, effective insect pest management requires the integration of control methods. It is important in the development of management strategies to identify interactions among control methods and natural processes. In this way, undesirable economic and environmental costs resulting from incompatibility of methods can be minimized.

Recent studies have shown that foliage-foraging ants are important predators of larvae and pupae of western spruce budworm, Choristoneura occidentalis Freeman, at least among populations in the Pacific Northwest (Campbell and Torgersen 1982, Campbell et al. 1983, Youngs and Campbell 1984). Unfortunately, carbaryl--the insecticide used in both 1982 and 1983 to control an outbreak of western spruce budworm in eastern Oregon--is also known to be capable of adversely affecting populations of at least some of these predaceous ants (Roush and Akre 1978). Thus, the carbaryl treatment in 1983 provided an opportunity to further evaluate some effects of this material on forest ants.

The objective of this study was to determine the effects of the carbaryl treatment of western spruce budworm on the foraging activity of forest ants.

METHODS

Study Areas. Four 0.75-ha plots in the Bear Valley Ranger District, Malheur National Forest, Oregon, were selected for study. All plots had high larval densities of western spruce budworm, and were similar in elevation, slope, aspect, and cover type; variation between plots resulting from habitat differences was thus minimized. Two plots, Dan's Creek and Murderer's Creek, were in areas treated with carbaryl and two plots, Starr Ridge and Herberger Spring, were in untreated areas.

Sampling. Ant foraging activity was determined from samples taken before and after the helicopter spraying of carbaryl on 6 July. Arboreal foragers were sampled with 30-by 60-cm rectangular sticky drop traps placed under the live crowns of Douglas-fir, Pseudotsuga menziesii var. glauca (Beissn.) Franco, and grand fir, Abies grandis (Dougl.) Lindl. in the manner described by Youngs and Campbell (1984). Forty-eight drop traps were used per site, with three traps placed under each of sixteen trees arranged in clusters of four. Ants were collected from the drop traps

soon after sunrise on the fourth day after the traps were set out.

Ground foragers were collected with a small portable vacuum (Paul and Mason 1985) from 20- by 20-cm baited boards. Twenty-five baited boards were set at 14.4-m intervals in a grid covering .33-ha within each plot. Baits of 50-g of canned catfood were placed on the boards early in the morning before ant activity began. Ants were collected from the surface of the boards later in the day, when temperatures were between 14⁰ C and 26⁰ C. The baited boards were not sampled when the sky was overcast.

Each plot was sampled with both drop traps and baited boards at least twice before the carbaryl treatment. A third prespray baited board sample was taken from the two untreated plots. After the treatment, each plot was sampled four times with drop traps and seven times with baited boards.

Ants collected from baited boards were placed in 70 per cent alcohol and taken to the laboratory for later identification. Ants caught in the sticky material on the drop traps were placed in styrofoam cups and taken to the laboratory. There, the sticky material was dissolved in kerosene warmed in a water bath. The ants were then placed in alcohol. Specimens were identified using keys (Creighton 1950, Francoeur 1973, Gregg 1963, Shattuck 1985, Wheeler and Wheeler 1963) and from comparisons with voucher specimens

housed at the USDA Forestry and Range Sciences Laboratory,
La Grande, Oregon, and at the Systematic Entomology
Laboratory, Oregon State University, Corvallis, Oregon.

RESULTS

We sampled for eight weeks, between 20 June and 16 August. We collected 10,486 ants from drop traps, and 3,001 ants from baited boards. Of nineteen species collected from the study areas, nine were common among sites on baited boards, and five were common among sites on drop traps. All species, listed by collection method, appear in Table I.

We subdivided the common species into two groups based on their tendency to prey on western spruce budworm. We defined budworm predators as those species that consistently prey on western spruce budworm, and budworm nonpredators as those species that are sporadic or unrecorded budworm predators. We based these classifications on our own observations and from data presented by Youngs and Campbell (1984).

We eliminated Formica manni from the analyses. This species was represented by a single specimen collected from a baited board on 22 June. The baited board was immediately adjacent to a clearing popularly used as a parking area for recreation. Formica manni is considered a desert species

(Creighton 1950) and is not usually found in forests. Our collection of F. manni was probably accidental.

Baited board Samples. We used Yate's corrected chi-square analysis of contingency tables to compare pre- and posttreatment means of ants per sample between sites. We pooled data into treated and untreated categories when the appropriate populations were homogeneous. The common budworm nonpredators collected from baited boards were Leptothorax muscorum, L. rugatulus, Myrmica emeryana, Tapinoma sessile, and Formica lasioides. Common budworm predators were Camponotus modoc, C. vicinus, Formica accreta, and F. neorufibarbis. Test results are summarized in Table II.

Drop Trap Samples. We examined trends in ant foraging activity with regression analysis. We used two-tailed t-tests to determine the significance of the slopes of the regression lines and to compare slopes between different regressions (Dixon and Massey 1983). Regression data are summarized in Tables III and IV.

When all species at each site were considered, the rate of foraging (indexed by the regression slope) during the sampling period decreased significantly at Dan's Creek and at Murderer's Creek. At Starr Ridge and at Herberger Spring, the rate of foraging remained about the same. Regression slopes were not significantly different between Dan's Creek and Murderer's Creek, nor between Starr Ridge

and Herberger Spring; therefore, we pooled data into treated and untreated categories. On treated sites the foraging rate decreased significantly during the sampling period. There was no significant change in foraging rate at untreated sites. The difference between slopes of the treated and untreated regression lines was significant ($p < .05$). Overall, the rate of ant foraging decreased nearly 200 per cent faster at the treated sites than at the untreated sites. Comparisons of treated and untreated regressions for all species combined are illustrated in Figure I.

Five of the fifteen species caught on drop traps were common among plots. Four of the common species were budworm predators: Camponotus modoc, C. vicinus, Formica accreta, and F. neorufibarbis. The lone budworm nonpredator common among plots was Formica lasioides. Of the total number of ants captured on drop traps, 97.2 per cent were these common species. Budworm predators comprised 95.9 percent of the overall total and 98.6 per cent of the common species total.

The numbers of Formica lasioides captured were relatively small; thus, we analyzed those data with contingency tables (Table V). Differences in pre- and posttreatment means were not significant between the two treated sites nor between the two untreated sites. Analysis of the pooled data showed that pre- and posttreatment means were significantly different between treated and untreated

areas. Foraging activity increased at both treated and untreated areas after the spray; however, postspray activity increased 800 per cent at the untreated sites, but only six per cent at the treated sites.

We used regression analyses to examine differences in foraging rates for Camponotus modoc, C. vicinus, Formica accreta, and F. neorufibarbis (Table III.). As before, we compared slopes of the regression lines and pooled data when appropriate. The foraging rate of F. neorufibarbis was significantly different on both untreated sites; thus, we could not pool those data into an untreated category. Indeed, foraging rates of F. neorufibarbis were similar between Murderer's Creek (treated) and Herberger Spring (untreated) ($t=-0.5822, p>.10$). The foraging rate of C. modoc at treated sites decreased an additional 900 per cent relative to the decrease at untreated sites. The rate of F. accreta foraging at treated sites decreased an additional 200 per cent relative to that at untreated sites. Camponotus vicinus foraging, however, decreased only 11 per cent at treated areas relative to untreated areas. Comparisons of treated and untreated regressions for C. modoc, C. vicinus, F. accreta are shown in Figures II.-IV.

DISCUSSION

Ant foraging is affected by variables such as local weather, patchiness of resources, and patterns of direct sunlight and shade. We interpreted low r-squares from our regressions as reflecting the inadequacy of a single variable, time, to fully explain changes in ant activity. Those regressions with relatively high r-squares were nearly all from treated plots. This suggests carbaryl spraying impacted foraging to the extent that factors besides time became relatively unimportant.

We inferred effects from the carbaryl treatment only in those species common among plots, with similar activity between the two treated plots and between the two untreated plots and which showed dissimilar activity between treated and untreated areas. Among ground foragers, budworm predators were the only species clearly affected by the carbaryl spray. Numbers of ground foragers captured on postspray treated plots were too low to examine spray effects on individual species. Arboreal foragers--nearly all budworm predators--also showed an overall decrease in foraging on postspray treated sites. The species Camponotus modoc and Formica accreta both showed significant decreases in postspray foraging on treated plots. Camponotus vicinus showed no such decrease, and variation in Formica neorufibarbis foraging was not clearly linked with the

carbaryl spraying. These four species prey on budworm pupae (Youngs and Campbell 1984); however it is not clear to what extent they prey on budworm larvae. We did not see large numbers of dead ants in the study sites, nor did ants coming in contact with carbaryl residues appear to be affected. Indeed, we saw many ants carrying killed budworm larvae back to nests for at least two days after the spray. Apparently, the carbaryl did not act as a contact poison on the ants, nor did it inhibit budworm predation. Perhaps those species affected by the spraying have a greater tendency to prey on budworm larvae; hence, they ingested more poisoned prey.

Campbell et al. (1983) suggest that ants affect the population dynamics of the western spruce budworm through their destruction of pupae. Our data indicate that for the species and species groups affected by the spraying, foraging was reduced for at least eight weeks--long enough for the budworm population to attain the pupal stage with reduced predation pressure from ants. In sprayed areas, survival rates of budworm pupae could possibly be higher than in nonsprayed areas with comparable ant and budworm densities. This may contribute to resurgence of some budworm populations.

SUGGESTIONS FOR FUTURE RESEARCH

Ant colonies commonly exist for several years. It is not clear whether those ant species with reduced foraging activity suffered permanent colony damage or temporary loss of workers. Ant sampling should be repeated in the year following insecticide application to determine long term effects.

At present, there is no adequate method for quantifying ant population density. Developement of such methods would increase our understanding of ant-budworm interactions and could perhaps lead to the manipulation of ant populations for their predatory effect on forest insect pests.

SUMMARY

Effects of carbaryl on the foraging activity of forest ants were studied during the insecticide treatment of a western spruce budworm outbreak in the Malheur National Forest in Oregon. Differences in foraging activity were determined from samples taken before and after the carbaryl treatment. Arboreal foragers were sampled with drop traps. Ground foragers were sampled from baits. All species or species groups that showed decreased foraging as a result of the treatment were budworm predators. One budworm predator species showed no change in foraging. One budworm nonpredator species showed increased foraging after the treatment. Reduced ant predation on budworm pupae may contribute to resurgence of some budworm populations.

MANUSCRIPTS PLANNED

This paper was prepared in partial fulfilment of the requirements for the Master of Science degree at Oregon State University. A thesis including this work is in preparation.

LITERATURE CITED

- Campbell, R.W., T.R. Torgersen. 1982. Some effects of predaceous ants on western spruce budworm pupae in northcentral Washington. *Environ. Entomol.* 11:111-114.
- Campbell, R. W., T. R. Torgersen, and N. Srivastava. 1983. A suggested role for predaceous birds and ants in the population dynamics of the western spruce budworm. *For. Sci.* 29:779-790.
- Creighton, W. S. 1950. The ants of North America. Harvard Univ., Museum of Comp. Zool. Bul. 104:1-585.
- Dixon, W. J. and F. J. Massey, Jr. 1983. Introduction to statistical analysis. McGraw-Hill, Inc., New York. 678pp.
- Francoeur, A. 1973. Revision taxonomique de especes Nearctique du groupe fusca, genre Formica (Formicidae, Hymenoptera). Societe Entomologique du Quebec, Memoire No.3.

Gregg, R. W. 1963. Ants of Colorado. Univ. of Colorado Press, Boulder, Colorado. 792pp.

Paul, H. G. and R.R. Mason. 1985. A portable vacuum for collecting arthropods from drop cloths. USDA Forest Service PNW For. and Rang. Exp. Stat. Res. Note PNW-421, March 1985.

Roush, C. F. and R.D. Akre. 1978. Impact of chemicals for control of the Douglas-fir tussock moth upon populations of ants and yellowjackets (Hymenoptera:Formicidae, Vespidae). Melanderia 30:95-109.

Shattuck, S.O. 1985. Illustrated key to ants associated with western spruce budworm. USDA Forest Service Agriculture Handbook No. 632.

Wheeler, G.C. and J. Wheeler. 1963. The ants of North Dakota. Univ. of N. Dakota, Grand Forks. 326pp.

Youngs, L.C. and R.W. Campbell. 1984. Ants preying on pupae of the western spruce budworm, Choristoneura occidentalis (Lepidoptera:Tortricidae), in eastern Oregon and western Montana. Can. Ent. 116:1665-1669.

Table I. Ant species collected from study sites.

	Bait-boards				Drop traps			
	DC	MC	SR	HS	DC	MC	SR	HS
MYRMICINAE								
Aphaenogaster								
subterranea (Emery)	-	+	+	-	+	-	-	-
Leptothorax								
muscorum (Nylander)	+	+	+	+	+	-	-	-
nevadensis Wheeler	-	+	+	+	-	-	-	-
rugatulus Emery	+	+	+	+	-	-	-	-
Myrmica								
emeryana Wheeler	+	+	+	+	-	-	-	-
DOLICHODERINAE								
Tapinoma								
sessile (Say)	+	+	+	+	-	-	-	+
FORMICINAE								
Camponotus								
laevigatus (F. Smith)	+	-	+	+	+	+	+	-
modoc Wheeler	+	+	+	+	+	+	+	+
vicinus Mayr	+	+	+	+	+	+	+	+
Formica								
accreta Francoeur	+	+	+	+	+	+	+	+
argentea Wheeler	-	-	+	-	+	+	+	-
hewetti Wheeler	-	-	-	-	+	+	-	-
lasioides Emery	+	+	+	+	+	+	+	+
manni Wheeler	-	-	+	-	-	-	-	-
sp. (microgyna gr.)	-	+	-	-	-	+	-	-
neorufibarbis Emery	+	+	+	+	+	+	+	+
podzolica Francoeur	+	-	+	+	+	+	+	-
Lasius								
alienus (Foerster)	-	-	-	-	+	-	-	-
pallitarsis (Provancher)	-	+	+	+	-	-	+	+

DC=Dan's Creek, MC=Murderer's Creek, SR=Starr Ridge,
 HS=Herberger Spring, +=collected, -=not collected

Table II. Contingency analysis of bait-board pre- and posttreatment mean counts of ants/sample.

Group	Site	Pretreatment mean	Posttreatment mean	Chi-sq. (Yate's)	P
All species	DC	134.0	5.4	2.2653	>.05
	MC	411.0	5.6		
	SR	110.7	64.6	3.0218	>.05
	HS	167.7	139.6		
	Treated Control	545.0 278.3	11.0 204.2	253.4741	<.001
All common species	DC	133.0	5.2	0.0102	>.90
	MC	96.5	4.4		
	SR	100.0	50.2	4.7830	<.05
	HS	163.3	132.0		
Common non-predators	DC	24.5	1.2	0.3928	>.50
	MC	19.0	0.8		
	SR	46.7	26.0	6.3426	<.025
	HS	94.3	110.2		
Common predators	DC	108.5	4.0	0.0039	>.90
	MC	77.5	3.6		
	SR	53.3	24.2	0.7632	>.25
	HS	69.0	21.8		
	Treated	186.0	7.6	37.2612	<.001
	Control	122.3	46.0		

DC=Dan's Creek, MC=Murderer's Creek, SR=Starr Ridge, HS=Herberger Spring

Table III. Regression data for ant species from drop trap samples. All species: $\ln(\text{Ants/sample}) = a + b(\text{Julian date})$, Individual species: $\ln(\text{Ants/sample} + 1) = a + b(\text{Julian date})$.

Species	Site	a	b	t-value	P	r sq.
All species	DC	13.7607	-.0408	-3.8931	<.01	.79
	MC	14.9549	-.0470	-7.5242	<.01	.93
	SR	8.5267	-.0117	-1.3988	>.20	.33
	HS	8.7434	-.0143	-2.7500	>.05	.65
	TR	14.4386	-.0443	-5.9180	<.01	.89
	CO	8.6160	-.0128	-1.9672	>.20	.49
Camponotus modoc	DC	12.2106	-.0429	-3.24	<.05	.72
	MC	14.1147	-.0608	-4.01	<.05	.80
	SR	8.0004	-.0197	-3.10	<.05	.71
	HS	3.3871	-.0069	0.70	>.50	.11
	TR	12.4024	-.0464	-3.51	<.05	.75
	CO	5.1621	-.0045	-0.94	=.40	.18
Camponotus vicinus	DC	7.1343	-.0175	-1.22	>.20	.27
	MC	8.6614	-.0249	-2.71	>.05	.64
	SR	6.6787	-.0178	-1.51	>.20	.36
	HS	7.9586	-.0246	-2.09	>.10	.52
	TR	7.9565	-.0214	-1.93	>.10	.48
	CO	6.9663	-.0192	-4.76	<.01	.85
Formica accreta	DC	13.9152	-.0443	-3.46	<.05	.75
	MC	17.6237	-.0662	-7.73	<.01	.94
	SR	8.6633	-.0157	-1.99	>.10	.50
	HS	7.3573	-.0176	-1.72	>.10	.43
	TR	15.4490	-.0532	-5.42	<.01	.88
	CO	8.3546	-.0167	-2.37	>.05	.58
Formica neorufibarbis	DC	17.9297	-.0773	-4.88	<.01	.86
	MC	11.3342	-.0333	-4.43	<.05	.83
	SR	5.6048	-.0029	-0.27	>.79	.02
	HS	10.5989	-.0270	-3.54	<.05	.76

DC=Dan's Ck., MC=Murderer's Ck., SR=Starr Ridge,
HS=Herberger Spring, TR=Treated, CO=Control

Table IV. Comparisons of slopes of regression lines.

Species	Comparison	t-value	P
-----	-----	-----	-----
All species	DC = MC	0.5074	>.60
	SR = HS	0.2683	>.60
	TR = CO	-3.1599	<.05
Camponotus modoc	DC = MC	0.8895	>.30
	SR = HS	-1.5889	>.10
	TR = CO	-2.8839	<.05
Camponotus vicinus	DC = MC	0.4401	>.60
	SR = HS	0.4108	>.60
	TR = CO	0.1870	>.80
Formica accreta	DC = MC	1.4304	>.10
	SR = HS	0.1458	>.10
	TR = CO	-2.9796	<.05
Formica neorufi-	DC = MC	-2.5169	<.05
	SR = HS	1.8368	>.10

DC=Dan's Creek, MC=Murderer's Creek, SR=Starr Ridge,
HS=Herberger Spring, TR=Treated, CO=Control

Table V. Contingency analysis of drop trap pre- and posttreatment means of ants/sample for *Formica lasioides*.

Site	Pretreatment mean	Posttreatment mean	Chi-sq. (Yate's)	P
-----	-----	-----	-----	-----
DC	2.50	0.75	0.3658	>.50
MC	1.50	3.50		
SR	1.00	2.50	0.0845	>.75
HS	2.00	24.75		
Treated	4.00	4.25	4.1481	<.05
Control	3.00	27.25		

DC=Dan's Creek, MC=Murderer's Creek, SR=Starr Ridge,
HS=Herberger Spring

LN(MEAN ANTS/SAMPLE) ON DROP TRAPS

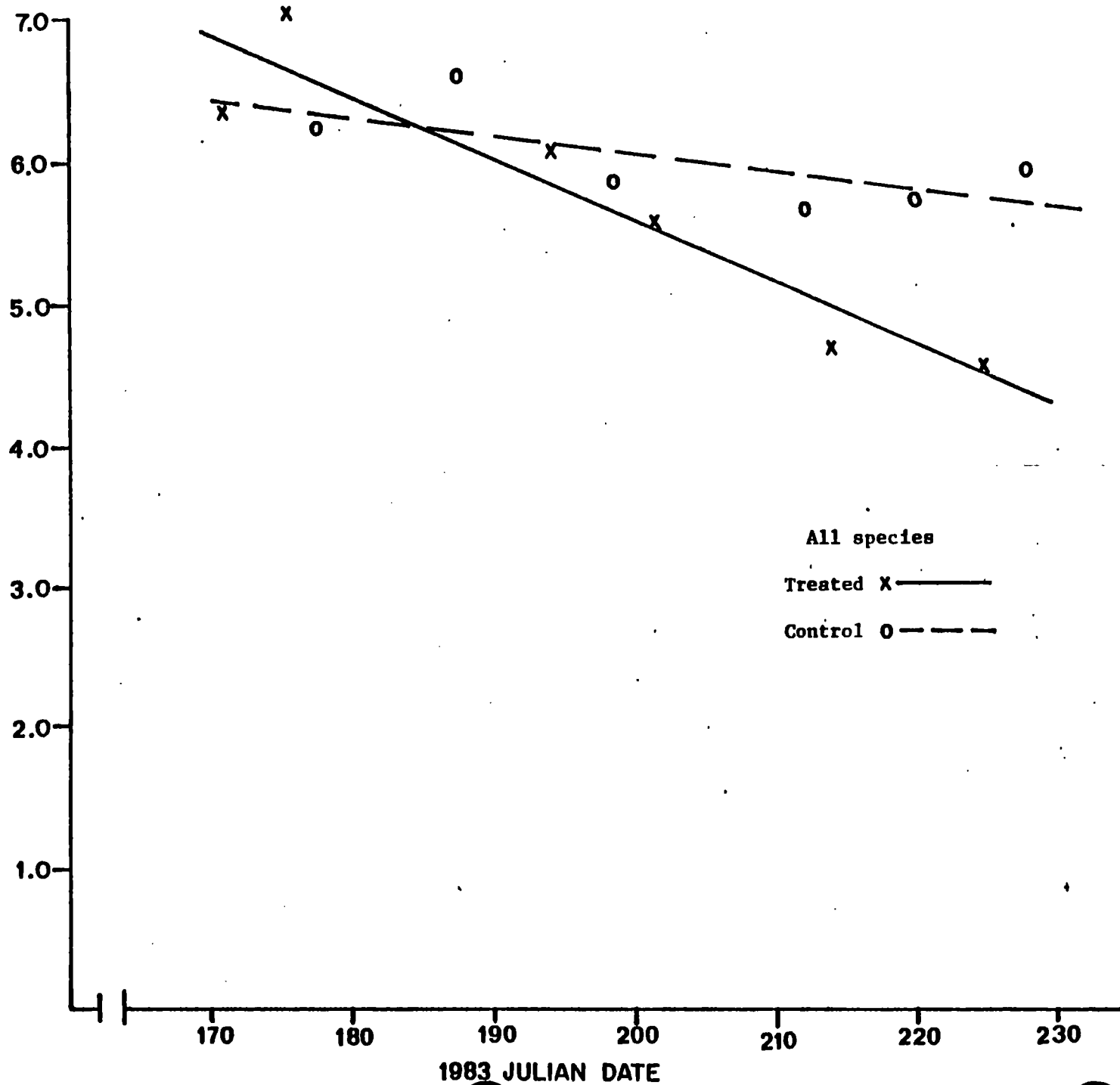


Figure I.

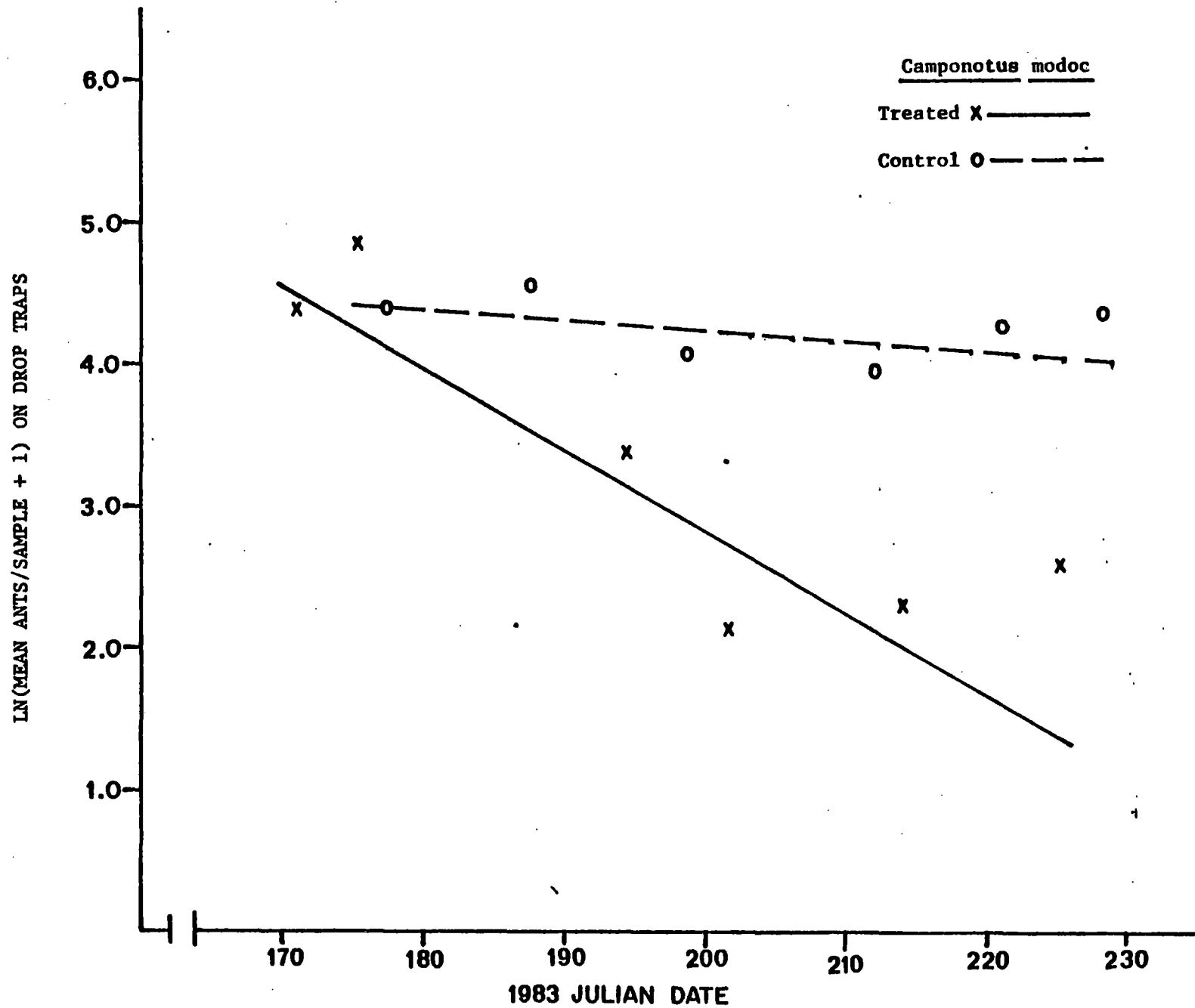


Figure II.

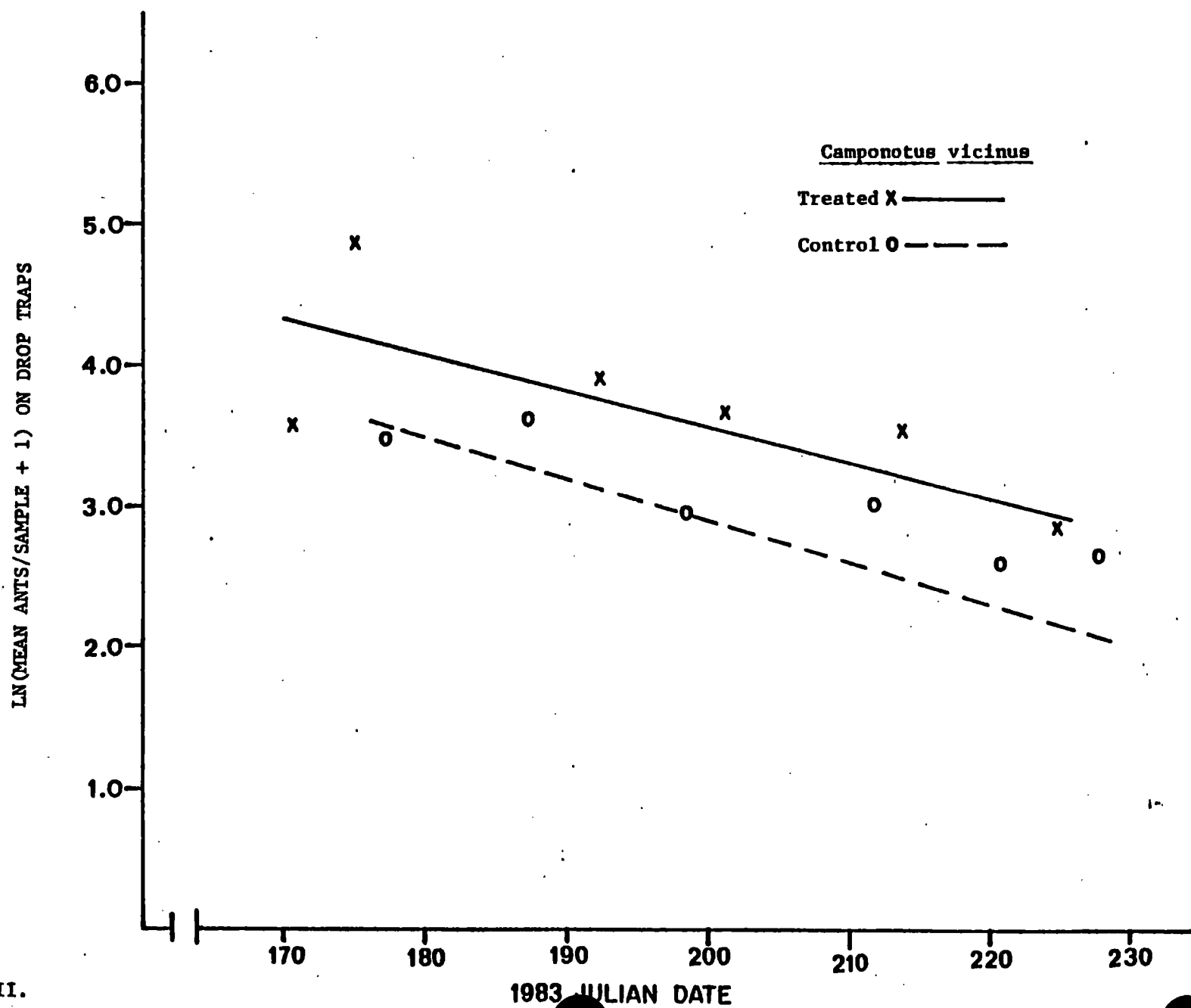


Figure III.

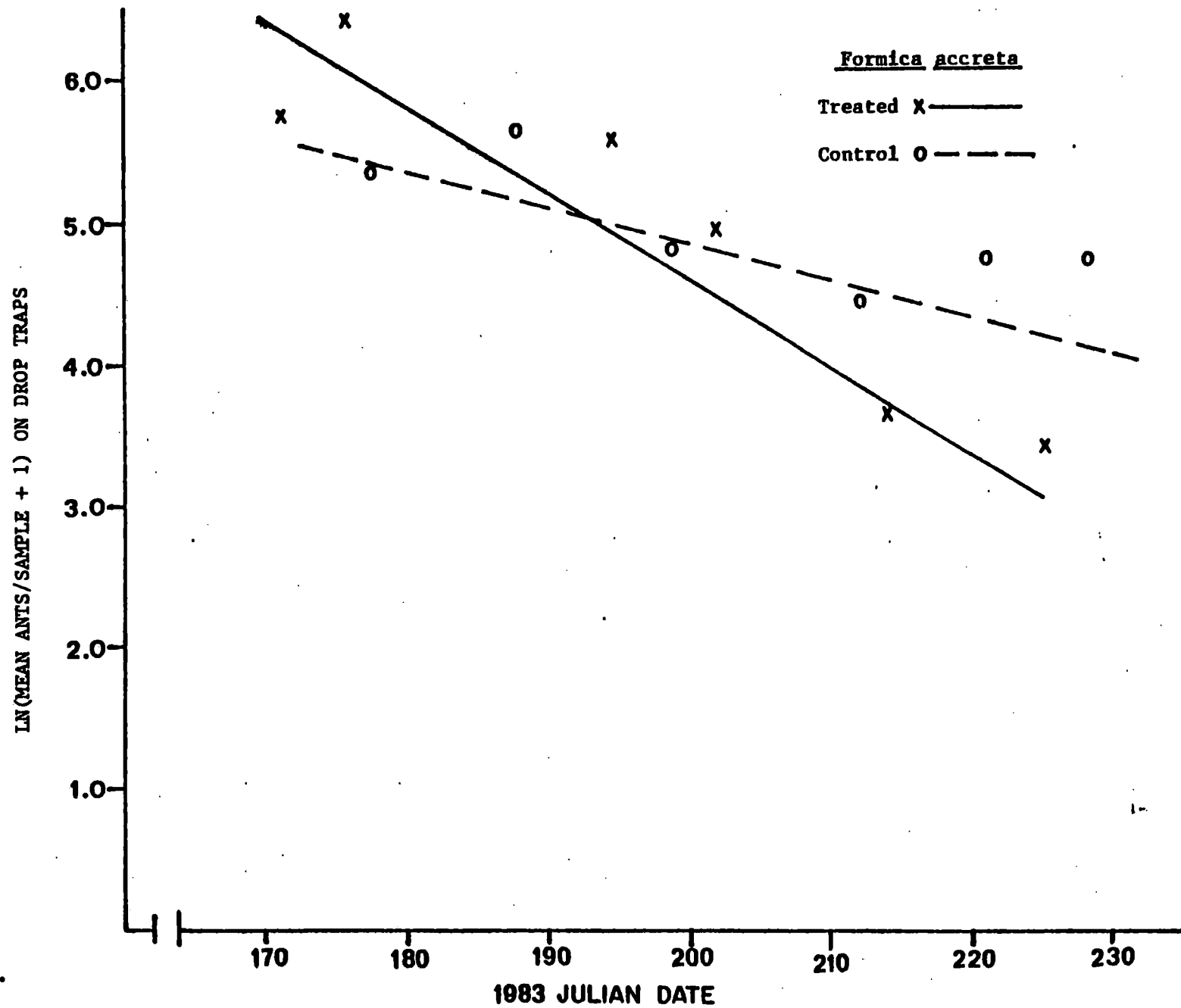


Figure IV.

Appendix II

Habitat Requirements of Foliage-foraging Predaceous
Woodland Ants in Eastern Oregon
and Western Montana

by

Lorna C. Youngs
Department of Entomology
Oregon State University
Corvallis, Oregon 97330

Currently: State Department of Agriculture
Plant Division (Entomology)
Salem, Oregon 97310-0110

and

Robert W. Campbell
State University of New York
College of Environmental Science and Forestry
Syracuse, New York 13210

Introduction

Predation by insectivorous birds and foliage-foraging ants is a significant mortality factor in the population dynamics of the western spruce budworm. These two groups of predators are the source of most of the mortality of budworm during the late larval and early pupal period, and may be the principal factor responsible for maintaining budworm populations at sparse densities (Campbell 1984).

Species of both Formica and Camponotus were active budworm predators in eastern Oregon and western Montana (Chapter III). The following species were identified as predators of budworm pupae: C. modoc, C. laevigatus, C. vicinus, F. obscuripes, F. podzolica, F. accreta, F. neorufibarbis, and F. lasioides. The dominant predators were the Camponotus species, especially C. modoc, together with F. obscuripes. Additional species of Formica and Camponotus have been observed or implicated as budworm predators - F. haemorrhoidalis in north-central Washington (Campbell and Torgersen 1982), F. criniventris in western Montana (Bain 1974) and F. subnuda, F. argentea and C. herculeanus in Idaho (Markin 1979).

Together, these studies show that the species complex of predaceous ants varies geographically. Any given site may have none or only a few of the species listed above. For the most part, these species were identified on sites selected for study of the population dynamics of the western spruce budworm. Thus, these studies reveal little about the distribution of these budworm predators throughout the range of the budworm.

There exists little information in the literature as well. Beyond broad geographic ranges gleaned from collection records and general descriptions of biology (Wheeler 1917, Mallis 1941, Cole 1942, Wheeler and Wheeler 1978), little is known about many of these species. Wheeler and Wheeler (1963) and Gregg (1963) give comprehensive reviews of the biology and distribution of ants in North Dakota and Colorado respectively, but similar treatments are lacking for many areas of the west.

We initiated this study to provide information about the distribution of ants predaceous on the budworm, at least for 2 areas in the western United States. We wished to determine if the species complex of ants foraging in the forest canopy changed over the range of environmental conditions inhabited by the budworm, to describe the distribution of each species, and to determine if these distributional patterns are related to environmental variables. We also wished to know if the density of ants foraging in the tree canopy changed along environmental gradients.

We conducted the study in eastern Oregon in the Elkhorn and Blue Mountains of the Willowa Whitman National Forest and in western Montana in the Lolo National Forest near Seeley Lake and the Lubrecht Experimental Forest, northeast of Missoula. These areas are well within the range of the budworm. In each state, we examined the pattern of distribution of potential budworm predators over a range of conditions represented by a moisture-temperature gradient. We selected 24 sites of varying environmental conditions in each state and sampled the foliage-foraging ant species as well as several site and stand variables on each site.

Site Description - Montana

We chose the 24 sites to represent both mesic conditions and extremes of moisture and temperature. Environmental conditions at each site were indexed by vegetation. We used the habitat type vegetational classification system of Pfister et al. (1977) for site selection and to determine the relative position of each site on a moisture-temperature gradient. In this region of Montana, the general progression of climax tree species with increasing moisture and decreasing temperature (increasing elevation) is as follows: ponderosa pine, Douglas-fir, grand fir, subalpine fir.

The 24 sites were divided among 4 habitat types, 6 sites per type. The habitat types were: Pseudotsuga menziesii/Symphoricarpos albus (PSME/SYAL h.t.) representing the warm-dry extreme of the moisture-temperature gradient; Pseudotsuga menziesii/Vaccinium

globulare (PSME/VAGL h.t.) and Abies lasiocarpa/Clintonia uniflora (ABLA/CLUN h.t.) representing mesic conditions; and Abies lasiocarpa/Menziesia ferruginea (ABLA/MEFE h.t.) representing the cold-wet extreme of the moisture-temperature gradient. All 4 habitat types are within the range of types inhabited by western spruce budworm (Fellin et al. 1983).

The following general description of these 4 habitat types is given by Pfister et al. (1977). The PSME/SYAL h.t. is common in Montana and found on moderately warm slopes and benches. Ponderosa pine is a major seral dominant, while lodgepole pine and western larch are essentially absent. The PSME/VAGL h.t. is found on relatively cool sites in the Douglas-fir series and is usually bordered upslope by the subalpine fir series. PSME/VAGL h.t. is a major type on the Lolo National Forest, occurring on well drained soils. Lodgepole and ponderosa pine and western larch are major seral dominants. The ABLA/CLUN h.t. is a relatively warm, moist type in the subalpine fir series, and is found extensively in northwestern Montana in river drainages. It is a very diverse habitat type with 5 distinct phases. The major seral tree species are Engelmann spruce, Douglas-fir, western larch and lodgepole pine. The ABLA/MEFE h.t. occurs on cool, moist exposures at higher elevations and is frequently bordered downslope by ABLA/CLUN h.t. in northwestern Montana. Lodgepole pine, Douglas-fir and Engelmann spruce are the common seral components of this type, while subalpine fir dominates old growth stands.

The 24 sites were located in 3 areas: the University of Montana Lubrecht Experimental Forest (25 miles northeast of Missoula), the valley floor near Seeley Lake, and the lower slopes of the Mission Range near Grouse Creek (ca. 15 miles west of Seeley Lake). All plots in the PSME/SYAL and PSME/VAGL h.t.'s were on the Lubrecht Experimental Forest. The plots in the ABLA/CLUN h.t. were located near Seeley Lake and those in the ABLA/MEFE h.t. were located near Grouse Creek. Both areas are in the Lolo National Forest. A north-south moisture gradient exists between Seeley Lake, which is on the upper end of the Clearwater River drainage and the Lubrecht Experimental Forest located near the juncture of the Clearwater and

Blackfoot Rivers. Mean annual precipitation is 56.5 cm at Seeley Lake and 45.5 cm at the lower elevations of the Lubrecht Experimental Forest. Thus the subalpine fir series is encountered at much lower elevations near Seeley Lake than at the Lubrecht Experimental Forest.

The 6 sites within each habitat type were chosen to represent a range of site and stand conditions that may affect ant abundance. In particular, we wished to test the effect of varying degrees of canopy coverage, by selecting sites with similar slopes and aspects, but differing in percent canopy coverage. Thus within each habitat type, 3 sites were designated open stands and 3 sites were designated closed stands, although all stands were within the range of normal stocking for the habitat type.

General site and stand characteristics for each habitat type are summarized in Table IV.1. Sites in the PSME/SYAL h.t. were located in an area where the major portion of the overstory had been removed in the 1930's. Designated open stands had undergone subsequent selection cuts. Shrub and herb cover was generally low. Stands in the PSME/VAGL h.t. were dominated by Douglas-fir. Designated closed stands were undisturbed; designated open stands had undergone either selection cuts, or in one case, an overstory removal (resulting stand was 60 years old). Shrub and herb cover was high in all but the very dense stands. Most of the stands in the ABLA/CLUN h.t. were in early successional stages dominated by seral species and varied considerably among sites in percent species composition. Designated closed stands were mature with considerable deadfall. Designated open stands were either thinned or had undergone an overstory removal. Understory vegetation was extensive and diverse. Most stands in the ABLA/MEFE h.t. contained overmature lodgepole pine, much of it windthrown. Designated open stands had either been thinned or severe windthrow of lodgepole pine had opened the canopy. Shrub species dominated the understory vegetation with little variation in species composition among sites.

Site Description - Oregon

We chose 24 sites in Oregon to represent varying conditions along a moisture-temperature gradient, using the habitat type concept. Habitat types in the Douglas-fir, grand fir and subalpine fir series represented (in the order given) increasingly cooler, moister conditions. We chose 8 sites in each tree series, again with varying site and stand conditions, with one half of the stands designated as open and half designated closed. All sites were within the range of conditions inhabited by the western spruce budworm ^{/1}.

The 8 sites in the Douglas-fir series were in the Pseudotsuga menziesii/Symporicarpos albus (PSME/SYAL) habitat type described for the northern Willowa-Whitman National Forest as a warm, dry type with Douglas-fir and ponderosa pine in the overstory and a generally impoverished understory (Daubenmire and Daubenmire 1968, Johnson 1982). Sites in this type were all located ca. 10 miles southeast of Medical Springs in the Willowa-Whitman National Forest. General site characteristics are summarized in Table IV.2. Stands had undergone varying amounts of overstory removal. Understory vegetation was sparse, the percent cover of S. albus increased with increasing Douglas-fir.

The Douglas-fir series is poorly represented in the Willowa-Whitman National Forest (Franklin and Dyrness 1973). It is confined to a narrow band between ponderosa pine sites too dry to support Douglas-fir and sites with sufficient soil moisture for grand fir to establish. The 8 sites in the PSME/SYAL h.t. were located at the upper elevational limits of the type near the transition zone between the Douglas-fir and grand fir series.

The grand fir series covers extensive areas of midslope forests in the Willowa-Whitman National Forest (Franklin and Dyrness 1973). The 8 plots in this series are evenly divided between two habitat types, Abies grandis/Linnaea borealis (ABGR/LIBO) and Abies

^{/1} Daniel B. Twardus, Forest Pest Management, USDA Forest Service, Portland, Oregon. Personal communication.

grandis/Vaccinium membranaceum (ABGR/VAME). Both are mesic habitat types located on bottom to midslopes, with stands dominated by grand fir with varying mixtures of Douglas-fir, western larch, lodgepole and ponderosa pine and Englemann spruce. Understory vegetation is diverse and density depends on density of the tree cover (Hall 1973). Jonsson (1982) considered the ABGR/VAME h.t. seral to ABGR/LIBO h.t. in the northern region of Willowa-Whitman National Forest. He found in paired stands, that V. membranaceum, coverage was reduced and that of L. borealis increased with increasing crown closure.

Six out of 8 sites in the grand fir series were located on Mount Emily Road, 2 at Simerson Spring, 2 at Drumhill Ridge and 2 at Green Mountain. The remaining 2 sites were located on the Indian Creek Road near Grey's Mountain. All sites were in the Willowa-Whitman National Forest. General site characteristics are found in Table IV.2. Stand densities varied with the degree of past overstory removal. Three out of 4 designated open stands were in the ABGR/VAME h.t. and 3 out of 4 designated closed stands were in the ABGR/LIBO h.t. Understory species were diverse. Thus in the study area, the ABGR/VAME and ABGR/LIBO h.t.'s integrated depending largely on canopy closure and are treated as a single unit for the purposes of this study.

The remaining 8 sites, in the subalpine fir series, were in the Abies lasiocarpa/Vaccinium membranaceum h.t. (ABLA/VAME) described by Hall (1973) as located on mid to upper slopes on generally northern aspects. The type is dominated by subalpine fir, major seral components are Engelmann spruce and western larch. Presence of V. membranaceum indicates that this type has the warmest soils in upper forest zone. Density and composition of understory vegetation is again directly related to tree cover.

Six out of 8 ABLA/VAME h.t. sites were located on Indian Creek Road ca. 5 miles north of Point Prominence. The remaining 2 sites were located on Mt. Emily Road near Conklin Spring. All sites were in the Willowa-Whitman National Forest. Sites near Point Prominence were located in a cold air drainage indicated by the presence of V. scoparium Leiberg, which is common in colder habitat types at higher elevations and not usually associated with the ABLA/VAME h.t. General

site characteristics are found in Table IV.2. Stand composition varied considerably among sites and stand density depended on the intensity of previous logging.

Materials and Methods

Field Procedures

We established a 0.1 ha circular plot at each site and recorded the following data for each plot: elevation, slope, aspect, and ground configuration. Ground configuration was coded in 4 classes: convex, straight, concave and undulating; increasing values of configuration classes indicate potential for increasingly moist conditions. We ocularly estimated ground cover in 5 cover classes for: the combination of exposed mineral soil, bed rock, and loose rock, and for moss or lichens. Litter depth was estimated to the nearest cm.

On each plot, we tallied all trees over 1 m tall by species, height (2 m classes) and d.b.h. (10 cm classes). These data were used to generate two measures of stand density - basal area (m^2 of all trees and by species) and crown competition factor (all trees and by species). Crown competition factor (Krajicek et al. 1961) is a relative measure of stand density and is a summation over all trees of the percent of the area of the plot that would be covered by each trees crown if the tree were open grown.

We also measured canopy coverage of all trees with a spherical densiometer at plot center and at 8 equally spaced points, midway between plot center and perimeter. The mean and standard deviation of the 9 percent tree cover scores were recorded for each plot. Stand age was either recorded from available stand records or from increment bores of dominant and codominant trees.

We tallied all exposed woody debris over 10 cm in diameter by length (1 m classes) and diameter (10 cm classes) and assigned a decay class from 1 to 5 based on a classification system developed for Douglas-fir (Fogel et al. 1973). Decay class was based on condition

of the bark, texture and color of the wood, and presence of epiphytes, invading roots and fungi. We calculated a cylindrical overestimation of volume for each piece and totaled the volume for each decay class and for all woody debris.

Snags and stumps were also tallied by diameter (10 cm classes) and height (1 m classes) of exposed wood and assigned one of 9 decay classes (Maser et al. 1979) based on the presence of branches or bark and on the condition of the wood. In this classification, as in that for woody debris, increasing class values indicate increasing decay. Volume of snags and stumps was accumulated by decay class, then totaled.

We identified all understory shrub and herb species and assigned them a cover class by ocular estimation. Cover classes were: rare - 1%, 1-5%, 5-25%, 25-50%, 50-75%, 75-95%, and 95-100% (Pfister et al. 1977). Tree species were assigned cover classes on the same scale.

We dug 1 soil pit at each site to a depth of 70 cm, and recorded depth of the organic layer and the surface soil. The moist consistence and percent gravels (> 2 mm dia.) for the surface and subsurface soils were estimated in the field and soil samples were taken midway in the surface soil and at 70 cm for later texture analysis by the hygrothermometer technique. We recorded texture in 11 classes from sandy (class 1) to increasingly clayey (class 11) soils, and moist consistence in 6 classes from loose (class 1) to extremely firm (class 6) soils.

Aspect, slope and geographic position of each site was used to generate the potential solar radiation in megajoules/m² accumulated over the year on each plot ^{/2}. This variable replaced aspect in subsequent analyses because aspect is a circular rather than linear function, and because changes in aspect are reflected in corresponding changes in the potential solar radiation received on the plot.

We used sticky traps to sample ants foraging in the canopy on 4 trees in each plot. We divided plots into 8 wedges of equal area and

^{/2} Stuart Childes, Department of Soil Science, Oregon State University, Corvallis, Oregon. Personal communication.

compression of axis ends (Gauch 1982). This ordination served as a check on the accuracy of site selection by habitat type. Clustering of plots along ordination axes and the position of each plot with clusters would confirm that vegetation on the plots could be separated into groups and that plots had been accurately classified to groups. Ordination of plots provided unique scores (ordination score) for each plot along a continuous variable (ordination axis) enabling the examination of differences among plots within groups (habitat types). As an aid to interpretation of the axes, the ordination scores for each plot on the first two DCA axes were correlated with the site and stand variables measured on the plot.

The abundance of each common ant species (collected on $\geq 20\%$ of the plots) was graphed against habitat type for each state to determine the general pattern of species occurrence over the moisture-temperature gradient. We then correlated each common ant species (X ants/sample tree/sample period/plot) with site and stand variables over all plots to determine which variables were significantly related to the abundance of each ant species in the state. We undertook a second correlation analysis on only those plots where the species had been collected to determine which variables were significantly related to changes in ant abundance where the species was detected. All correlations were judged significant at the 0.05 level of probability.

The following site and stand variables were used in both correlation analyses: site variables - elevation, slope, ground configuration, total potential solar radiation (radiation), percent cover of mineral soil (% mineral soil), percent cover of moss or lichen (% moss), and average litter depth; stand variables - stand age, total basal area, crown competition factor (CCF) and % canopy cover; dead wood variables - total volume of downed woody debris (woody debris) and total volume of snags and stumps (snags and stumps); soil variables - depth of organic layer (organic depth), depth of surface soil (surface depth), moist consistence surface soil (consistence-surface), texture of surface soil (texture-surface), percent gravels of surface soil (% gravel-surface), moist consistence

of subsurface soil (consistence-subsurface), texture of subsurface soil (texture-subsurface) and % gravels of subsurface soil (% gravel-subsurface).

We also correlated the abundance of each ant species with subsets of the above variables. The abundance of each ant species was correlated with the cover class of each understory species and the cover class of each tree species, to determine if the distribution of individual plant species was more closely related to that of the ant species than the pattern generated by ordination of all plant species. We also correlated the abundance of each ant species with the volume of woody debris and snags and stumps by decay class to determine if information had been lost when total volume was used in the analyses. We again determined significance at the 0.05 probability level.

To test the hypothesis that ants of all species are more common in stands with open canopies, we conducted a χ^2 test of independence on the total number of ants collected of each species in each habitat in each state in the designated open and closed stands. Additional χ^2 tests were performed on the number of ants of certain of the wood inhabiting species collected on plots categorized by volume of woody debris and snags and stumps.

Results - Montana

Site Ordination by Vegetation Composition

In the DCA ordination of plots by tree and understory vegetation, most of the variation was captured in the first 2 axes (eigenvalues for axes 1 and 2 were 0.545 and 0.219 respectively; eigenvalues of all subsequent axes were < 0.08). When plot scores on the first 2 axes are graphed (Fig. IV.1) the plots fall into 4 distinct clusters corresponding to the 4 habitat types.

Correlations between plot scores on the first ordination axis (DCA axis 1) show that total potential solar radiation increases with increasing plot scores, while elevation, slope and percent of the

ground covered by moss decreases (Table IV.3). Litter depth and depth of the organic soil layer also decrease as site scores increase. Thus the first DCA axis can be interpreted as a temperature-moisture gradient. Plots on the hot-dry end of the axis (PSME/SYAL h.t.) are lower in elevation, have high potential radiation values, and less accumulated litter or moss. Plots on the cool-wet end of the axis (ABLA/MEFE h.t.) are higher in elevation, have lower potential solar radiation values, and more moss and litter.

The second DCA ordination axis (DCA axis 2) separates the plots in the ABLA/CLUN h.t. from those in the PSME/VAGL h.t. which are intermingled on the first ordination axis (Fig. IV.1). Because of the north-south moisture gradient between Seeley Lake and the Lubrecht Experimental Forest, subalpine fir grows at much lower elevations at Seeley Lake. Thus mean elevation of the plots in the ABLA/CLUN h.t. are actually lower than those of all other habitat types. Mean potential solar radiation is the same for plots in both PSME/VAGL and ABLA/CLUN habitat types, as is litter depth and depth of the organic layer of the soil.

Plot scores on the second DCA axis are primarily correlated with soil characters and with ground configuration. Plots in the ABLA/CLUN h.t. are either concave or undulating and characterized by soils of varying silty to fine sandy alluvium which were generally poorly drained (Table IV.3). Thus the second DCA axis can be interpreted as a soil moisture gradient, with plots in the ABLA/CLUN h.t. on the wet end of the axis.

Distribution of Ant Species

Nine ant species were collected in sticky traps beneath sample trees, 4 Camponotus species - C. herculeanus, C. laevigatus, C. modoc and C. vicinus and 5 Formica species - F. accreta, F. curiosa Creighton, F. hewitti Wheeler, F. neorufibarbis and F. podzolica. The most commonly encountered species (collected on 20% or more of the plots) were C. herculeanus, C. modoc, C. vicinus, F. neorufibarbis and F. podzolica. C. laevigatus, F. curiosa and F. hewitti were each

subsets of the environmental variables showed no significant correlations between C. vicinus and the volume of woody debris in any decay class. However, C. vicinus was significantly correlated with the percent cover of ponderosa pine and 3 understory species:

Achillea millefolium L., Balsamorhiza sagittata (Pursch) NuH., and Festuca scabrella Torr. Significantly, more C. vicinus were collected in designated open plots than closed plots (Table IV.5).

Significant correlations between habitat variables and the abundance of C. modoc are given in Table IV.4. The abundance of C. modoc was not correlated with the volume of dead wood in any decay class. The percent cover of Douglas-fir and the understory species Antennaria racemosa Hook., and Berberis repens were significantly correlated with the abundance of C. modoc. Significantly more C. modoc were collected in designated open plots in both PSME/VAGL and the ABLA/MEFE h.t.s (Table IV.5).

Significant correlations between the abundance of C. herculeanus and habitat variables are shown in Table IV.4. C. herculeanus was not correlated with the volume of dead wood in any decay class or with the percent cover of any tree species. Its abundance was correlated with the percent cover of the understory shrubs, Menziesia ferruginea and Vaccinium scoparium. More C. herculeanus were collected on open plots in the ABLA/MEFE h.t. but the reverse occurred in the ABLA/CLUN h.t. (Table IV.5).

Habitat variables significantly correlated with the abundance of F. podzolica are shown in Table IV.6. Formica podzolica nests in the soil, thus correlations with volume of woody debris by decay class were not tested. F. podzolica was significantly correlated with the total basal area of Pinus contorta and negatively correlated with % cover of Pseudotsuga menziesii. F. podzolica was positively correlated with the % cover of 13 understory species; highest correlations were with, Anaphalis margaritacea (L.) B & H, Calamagrostis canadensis, Clintonia uniflora, Cornus canadensis, Equisetum sp., Galium boreale, Osmorhiza chilensis, Prunella vulgaris L., and Smilacina stellata (L.) Desf. More F. podzolica were

collected on open plots in the ABLA/CLUN h.t. while the reverse occurred in the PSME/SYAL h.t. (Table IV.5).

The abundance of F. neorufibarbis was significantly correlated with just 4 habitat variables (Table IV.6). Although the abundance of this species was not significantly correlated with any category of wood or decay class, significantly more ($\chi^2=76$) were collected on plots with high volumes of woody debris (mean 130 m³/ha), than low volumes (mean 66 m³/ha) in the ABLA/MEFE h.t. The reverse was true in the ABLA/CLUN h.t. where significantly more ($\chi^2=35$) were collected on plots with low volumes of woody debris (mean 24 m³/ha) than plots with high volumes (mean 130 m³/ha).

The abundance of F. neorufibarbis was not significantly correlated with the percent cover of any tree species and with only one understory species - Vaccinium scoparium. More individuals were collected in open stands in all but the ABLA/CLUN h.t. (Table IV.5).

Results - Oregon

Site Ordination by Vegetation Composition

In the DCA ordination of plots by tree and understory species cover classes, most of the variation was captured in the first two axes (eigen values were 0.650 and 0.192 respectively, eigen values for all subsequent axes were < 0.09). When plot scores on the first two axes are graphed (Fig. IV.3), plots fall into 3 clusters corresponding to habitat types in the 3 tree series. The tight clustering of plots in the grand fir series justifies the grouping of the two grand fir habitat types in this study. Plots 17 and 18 in the ABLA/VAME h.t. were on Mt. Emily and had a more heterogenous understory than the remaining subalpine fir sites located ca. 25 miles to the east on Indian Creek Road.

The first DCA axis was positively correlated with total potential solar radiation and percent of the plot covered by exposed mineral soil and negatively correlated with percent area covered by moss or lichen and elevation (Table IV.7). Thus plots become progressively

warmer and drier with increasing site scores and this axis can be interpreted as a moisture-temperature gradient. The hot-dry end of the axis is once again represented by plots in the PSME/SYAL h.t.

The second DCA axis further separates the plots in the subalpine fir series from those in the grand fir series. Correlations with elevation and potential solar radiation but not with percent area covered by moss (Table IV.7) indicate that this axis can be interpreted more as a temperature gradient than a temperature-moisture gradient.

Distribution of Ant Species

Eleven species were collected on sticky traps beneath sample trees: 4 Camponotus species--C. herculeanus, C. laevigatus, C. modoc and C. vicinus--and 7 Formica species--F. accreta, F. argentea, F. haemorrhoidalis, F. lasioides, F. neorufibarbis, F. obscuripes, and F. podzolica. The most commonly encountered species (collected on 25% or more of the plots) were C. modoc, C. vicinus, F. accreta, F. neorufibarbis and F. podzolica. F. haemorrhoidalis was collected on 1 plot and F. argentea on 2 plots in the PSME/SYAL h.t. C. laevigatus and F. lasioides were collected on 1 plot in the PSME/SYAL and ABGR/LIBO - ABGR/VAME h.t.s. F. obscuripes was collected on 1 plot in the grand fir and subalpine fir habitat types and C. herculeanus was collected on 1 plot in the subalpine fir habitat type.

The most species were collected in the PSME/SYAL h.t., where all but C. herculeanus and F. obscuripes were collected. The greatest number of ants were also collected in that habitat type. The fewest species (5) and fewest individuals were collected in the subalpine fir habitat type. Eight species were collected in the grand fir habitat types.

With the exception of F. neorufibarbis, there was a general decrease in the number of individuals collected of the 5 common species with increasingly cool and moist conditions (Fig. IV.4). C. vicinus was collected on all plots in the Douglas-fir habitat type and 1 plot in the grand fir habitat types. C. modoc was collected on 7 plots in the Douglas-fir habitat type, all plots in the grand fir

types and 2 subalpine fir plots. F. accreta was collected on all Douglas-fir plots, and 4 plots in the grand fir habitat types. F. neorufibarbis was collected on 3 Douglas-fir, 7 grand fir plots and 5 subalpine fir plots.

The mean number of C. modoc per sample per plot was correlated ($r=.631$, $P < .05$) with the mean number of F. neorufibarbis and with the mean number of F. accreta ($r=.730$, $P < .05$). There were no significant correlations among the abundances of any other species.

More ants were caught in the first sample period (July 9-13) in the following species: C. modoc - 63%, F. accreta - 54%, and F. neorufibarbis - 80%. More C. vicinus (63%) and F. podzolica (65%) were caught in the second sample period (July 29 - August 7).

Correlations Among Common Species and Environmental Variables

Significant correlations between the abundance of C. vicinus and habitat variables are shown in Table IV.8. C. vicinus was also correlated with the percent cover of ponderosa pine and 4 understory species: Achillea millefolium, Carex geyeri, Cerocarpus ledifolius, and Symphoricarpos albus. The abundance of C. vicinus was not significantly correlated with the volume of wood in any decay class. There was no difference in the number of ants collected in open or closed stands (Table IV.9).

The abundance of C. modoc over all plots was correlated with few site and stand variables (Table IV.8). The volume of dead wood in any decay class was not significantly correlated with the abundance of C. modoc. When the volume of woody debris and of snags and stumps were classified into 2 groups on the grand fir plots, significantly more C. modoc were collected in the high volume classes ($\text{Chi}^2 = 44.4$ and $\text{Chi}^2 = 62.9$, mean volume for woody debris = $169 \text{ m}^3/\text{ha}$ and $63 \text{ m}^3/\text{ha}$ for snags and stumps) than in the low volume classes (mean volume = $54 \text{ m}^3/\text{ha}$ and $28 \text{ m}^3/\text{ha}$ respectively). The reverse occurred on the Douglas-fir plots. More C. modoc were collected in the low volume classes ($\text{Chi}^2 = 163$ for woody debris and for snags and stumps). Mean volume of woody debris for low and high classes was

38 m³/ha and 90 m³/ha and mean volume for snags and stumps for low and high classes was 4 m³/ha and 28 m³/ha. Significantly, more C. modoc were collected in plots with open canopies in both the Douglas-fir and the grand fir habitat types (Table IV.9).

Significant correlations between the abundance of F. accreta and habitat variables are given in Table IV.10. The abundance of F. accreta was correlated with the percent cover of ponderosa pine and with 3 understory species: Berberis repens, Carex geyeri, and Hieracium albiflorum. Significantly more F. accreta were collected in open stands in both the Douglas-fir and grand fir plots (Table IV.9).

Habitat variables correlated with the abundance of F. podzolica are shown in Table IV.10. The abundance of F. podzolica was correlated with the percent cover of ponderosa pine and 4 understory species - Achillea millefolia, Arnica cordifolia, Collomia grandiflora Dougl., Nutt. and Symphoricarpos albus. Although more F. podzolica were collected in closed stands in both the Douglas-fir and grand fir habitat types, the species was collected in so few plots in each habitat type, that a Chi² analysis was not attempted.

The abundance of F. neorufibarbis over all plots was significantly correlated with only one habitat variable (Table IV.10). The abundance of F. neorufibarbis was not significantly correlated with the volume of dead wood in any decay class. However, if the volume of woody debris and of snags and stumps on each plot in the grand fir habitat type are divided into 2 classes, then the number of ants collected the high volume class of woody debris (mean volume - 169 m³/ha) and of snags and stumps (mean volume - 63 m³/ha) is significantly greater (Chi² = 172 and Chi² = 94 respectively) than in the low volume class of woody debris (mean volume 54 m³/ha) and snags and stumps (mean volume = 28 m³/ha). The reverse situation occurred on the plots in the subalpine fir series. Significantly more ants were collected in the low volume class of woody debris (mean volume = 59 m³/ha, Chi² = 5.8) and of snags and stumps (mean volume = 26 m³/ha, Chi² = 48.8) than in the high volume classes (mean volume = 233 m³/ha and 132 m³/ha respectively).

The abundance of F. neorufibarbis was not significantly correlated with the percent cover of any tree species, but it was significantly correlated with the percent cover of 8 understory species - Bromus sp., Chimaphila umbellata, Galium triflorum, Linnaea borealis, Ranunculus uncinatus D. Don, Ribes sp., Rosa sp. and Smilicina stellata. Significantly more F. neorufibarbis were collected in stands in the low canopy cover class in all habitat types (Table IV.9).

Discussion

Distribution of Common Species

With the exception of a few individuals of the genera Lasius and Myrmica, the complex of ants foraging in the canopy on the plots in both states was composed of species of either Camponotus or Formica. Although 9 species of these two genera were collected in Montana and 11 species were collected in Oregon, only 6 species could be considered common. All of the common species prey on budworm.

Four out of the 6 species were common to both states. Some correlations exist between the pattern of distribution of a few species, but the correlations are unique to one or the other state. In a state, each species had a unique distributional pattern across the range of habitat types we studied, and the pattern usually differed between states. The average abundance per plot of each species also differed between states as well as among habitat types. For most species, there was also considerable variation within habitat types. Thus the pattern of distribution of each species and the environmental variables that may be associated with this pattern must be evaluated individually.

Camponotus vicinus

With one exception in each state, C. vicinus was collected in only the warmest, driest habitat type - PSME/SYAL h.t. (This does not

imply that this habitat type is found under exactly the same conditions in both states. Although the name is used in several western states to describe the same general association of tree and understory species, regional differences exist in the environmental conditions represented by the type.) It is not surprising that the presence of C. vicinus is negatively correlated with elevation and positively correlated with total potential solar radiation in both states. The negative correlation with percent of plot covered by moss or lichen in Montana and depth of the litter layer in Oregon also indicate conditions found on warmer, drier sites. Although the soils in this habitat type differ between states (soils in Montana were generally firmer with a higher clay content and less coarse fragments) C. vicinus was consistently more abundant on plots with firmer soils of high clay content.

The positive correlation between the abundance of C. vicinus and the percent cover of ponderosa pine is to be expected since that tree species is also more common on warm-dry sites. The same can be said for the correlations with understory species. Although, except for Achillea millefolium, the species differ between states, in general, all are found more commonly in the PSME/SYAL h.t. than in the other habitat types examined.

Since few C. vicinus were collected on the Montana plots, and numbers varied little among plots compared to Oregon, discussion of factors related to abundance of this species is confined to the Oregon data. Within the range of conditions on the Douglas-fir plots, C. vicinus is still most abundant on the warmest-driest plots with the highest clay content. Unlike the other common species, the abundance of C. vicinus was not related to stand density.

Camponotus vicinus is member of the subgenus Tanaemyrmex Ashmead, most of the species of which nest in the soil or, rarely, buried wood. Members of this subgenus are generally found in the southern states, although C. vicinus has been recorded throughout the American Rocky Mountains and into Canada. Other researchers have also found it more common in warmer, drier forest sites (Wheeler 1917, Cole 1942, Wheeler and Wheeler 1963). Gregg (1963) reported that in Colorado C.

vicinus was collected in both open and wooded land, primarily deciduous or ponderosa pine - Douglas-fir stands but never in dense forests. He also found a correlation between the presence of C. vicinus and clay soils. Nesting sites were usually under rocks. Thus it appears that C. vicinus is limited to the warm-dry end of the range of conditions inhabited by the western spruce budworm.

Camponotus herculeanus

Camponotus herculeanus was the most commonly encountered species in Montana but virtually absent from Oregon. It was most abundant in the subalpine fir series in Montana, and the only Oregon collection was also in that series. Although the abundance of C. herculeanus was significantly correlated with elevation, the species was also common on the ABLA/CLUN h.t. plots which were at the lowest elevations. This probably reflects the adaptation of C. herculeanus to cooler-moister conditions (usually found at higher elevations) rather than to a relation with elevation alone. C. herculeanus nests in wood not in soil, thus the correlations with more friable soils of high gravel content reflect the occurrence of soils of this type in the ABLA/MEFE h.t. where C. herculeanus was most abundant.

Both the correlation analyses and the χ^2 tests of numbers caught in open and closed stands show that C. herculeanus is more abundant in stands of lower canopy coverage. Canopy coverage may have a greater effect on the abundance of C. herculeanus than the amount of available dead wood for nesting sites. It is also possible that the lack of correlation between the abundance of this species and the volume of dead wood is due to a threshold effect. The function may not be linear. Since no plot was completely lacking in woody debris, it may be that the availability of nesting sites was not a limiting factor.

C. herculeanus is a dominant ant in boreal and alpine forests of North America (Wheeler and Wheeler 1963). Gregg (1963) found this species abundant in cold coniferous forests in Colorado. Its upper range terminated at the timberline, where he stated that they were

limited by nesting sites. From collection records, he noted that C. herculeanus was found in wood of all stages of decay, but he did not quantify a preference for wood of a certain stage or the relation between ant abundance and amount of available nesting material.

Sanders (1964) investigated the biology of C. herculeanus in New Brunswick and noted that the species occupied diverse habitats and that its occurrence was not correlated with any discernable environmental variables. In later work in 3 successional stages of spruce-fir forest (Abies balsamea (L.) Mill. - Picea glauca (Moench, Voss), Sanders (1970) found more C. herculeanus in immature stands, where he speculated that the availability of woody debris made these stands attractive colonization sites.

Our work shows that, as in other areas, C. herculeanus is adapted to cold forests. Although rarely collected in Oregon, its distribution in Montana was sufficiently broad to prevent further conclusions about its habit preferences based on our data. We did find that its abundance at site is inversely related to stand density. We were not able to show a linear relationship with the abundance of available nesting material, due possibly to the threshold effect discussed above.

Camponotus modoc

Camponotus modoc was common in both states and was collected on more plots in Oregon than any other species. In both states it was most abundant in the more mesic habitat types although it was collected throughout the entire range. The one exception is its absence from the samples in the ABLA/CLUN h.t. Our data offered us no explanation for this and we can only speculate that this habitat type may be too wet for C. modoc.

The abundance of C. modoc is correlated with few environmental variables in either state and those that are significantly correlated vary between states. In both states the abundance of C. modoc is related to stand density and to the amount of dead wood available for nesting sites. Significantly more C. modoc were collected in more

open stands in all habitat types where it was common, and in Oregon both stand basal area and crown competition factor were negatively correlated with the abundance of C. modoc over all plots. In Montana, the abundance of C. modoc on plots where it was collected was significantly correlated with the volume of snags and stumps, while in Oregon more ants were collected in stands categorized as having high volume of dead wood, at least on the grand fir plots. Since the reverse was true on the Douglas-fir plots, it is possible that the effects of stand density and amount of available nesting material are so interrelated that our data are insufficient to clearly separate the two. The same phenomenon of a threshold effect for dead wood discussed above in C. herculeanus may also occur with C. modoc.

Several authors have reported C. modoc over a wide range of forest conditions (Wheeler 1917, Wheeler and Wheeler 1963, Gregg 1953, Cole 1942). Gregg (1963) reported that although the ranges of C. herculeanus and C. modoc overlap, C. modoc is generally found at lower elevations, a situation confirmed by our Montana data and to some extent our Oregon data. The distribution of C. modoc, like that of C. herculeanus is also too broad to produce strong correlation with most of the variables we measured. Where it was present, the abundance of C. modoc was directly related to the amount of available nesting sites (woody debris) and inversely related to stand density.

Formica accreta

Formica accreta was common in Oregon but rarely encountered in Montana. It was not collected in the cool subalpine fir habitat types in either state. The correlations between the abundance of F. accreta and environmental variables in Oregon are difficult to interpret. Although it undoubtedly nests in soil, only the analysis over all plots showed any significant correlation with soil variables (Table IV.10). Since the average values for depth of the organic and surface soil layers are lowest for the PSME/SYAL h.t. and F. accreta is most abundant in that type, correlations between soil variables and F. accreta may not be indicative of an association with shallow soils

with little accumulated organic matter. The negative correlation with stand age may also be due to the fact that stands in the PSME/SYAL h.t. were younger.

More ants were collected on plots with open stands than closed stands (Table IV.9) and those plots in general had more area covered by exposed mineral soil. Thus from our data we can conclude only that F. accreta is more abundant in the mesic to somewhat xeric range of environments inhabited by the budworm, and that factors such as stand density and soil depth may be related to changes in abundance.

Formica accreta was separated from F. fusca L., and raised to species rank in a taxonomic revision of the F. fusca species group (Francoeur 1973). Thus, there is very little information on the biology of F. accreta that can be separated from that recorded for F. fusca.

Formica podzolica

Formica podzolica was collected in both states on all but the coldest habitat type (ABLA/MEFE). Its distribution in all habitat types but the ABLA/CLUN is so scattered that it is difficult to determine factors related to that distributional pattern. This is especially so in Oregon where the numbers collected were generally low and the 6 plots where it was detected were scattered through all 3 tree series. The scarcity of the Oregon data makes the analysis in that state difficult and we will confine our discussion to the pattern of occurrence in Montana.

Certainly the high numbers of F. podzolica collected in the ABLA/CLUN h.t. created high correlations with the range of environmental variables in that type. Hence, high numbers of F. podzolica are associated with plots of low elevation, gentle slopes, sandy soils, and concave ground configuration - all characteristics of the ABLA/CLUN h.t. Even the majority of species significantly correlated with F. podzolica are more common in that habitat type. However, the negative correlation with stand age may reflect a relation independent of the influence of the high numbers of this

species in the ABLA/CLUN h.t., since average stand age in that type is mid range for all types. Thus, F. podzolica may be a pioneer species in Montana and more common in younger stands.

Francoeur (1973) also found F. podzolica widely distributed in many forest types and noted that the species was common in secondarily successional stands. He speculated that F. podzolica penetrated forested lands following silvicultural activity and was frequently found along forest roads. The greater number of ants found in open stands in Montana (Table IV.5) is in agreement with his general conclusion.

Francoeur also recorded a greater abundance of nests from sandy soils. The presence of high numbers of F. podzolica in the ABLA/CLUN h.t. may be related more to the nature of soils in that habitat type than other environmental variables. Thus, our data indicate that F. podzolica may be present throughout most of the range of habitat types examined, but that abundant populations are more common in open stands or younger stands with sandy soils.

Formica neorufibarbis

Although F. neorufibarbis is very common in both Oregon and Montana, little useful information resulted from the attempt to relate distribution and abundance to environmental variables. The lack of linear correlation with practically all the environmental variables in Oregon results from the high densities collected on the grand fir plots, which represent mesic conditions for most of the variables. In Montana, even though the numbers collected increase in increasingly cooler wetter habitat types, few variables are significantly correlated with ant abundance.

One of the few clear relations between F. neorufibarbis and environmental characteristics is with stand density; in all habitat types in Oregon and 2 out of 3 in Montana, significantly more F. neorufibarbis were collected in open stands. The percent canopy coverage was also negatively correlated with the abundance of F. neorufibarbis over all plots in Montana.

Wheeler and Wheeler (1963) and Francoeur (1973) consider F. neorufibarbis a dominant ant of boreal and alpine forests. Gregg (1963) reported the species from a wide range of forest types and found the species common even at high elevations. He considered F. neorufibarbis extremely cold tolerant. Our findings in Montana were consistent with his observations; highest numbers were collected in the coldest, highest elevational habitat type (ABLA/MEFE).

Francoeur also states that F. neorufibarbis is essentially a forest species. It nests commonly in rotten wood or organic material although it has been reported nesting in soil in western North America. Letendre et al. (1971) considers that distribution of the species at least in some areas of Quebec, may be limited by the availability of suitable nesting sites - woody debris. Although we found no significant correlations between the abundance of F. neorufibarbis and the volume of dead wood in any category or decay class, in both Montana and Oregon more individuals were collected on plots with high volumes of woody debris in the two habitat types where the species was most abundant (ABLA/MEFE and ABGR/LIBO - ABGR/VAME).

Thus we found F. neorufibarbis distributed throughout both areas where we worked and tolerant of the cold, wet conditions found in subalpine fir habitat types. Its abundance is inversely related to stand density and may be influenced by the availability of nesting material.

Distribution of All Species

In both Oregon and Montana, the mesic habitat types were richer in ant species and total numbers collected. While the number of species was reduced in habitat types representing more extreme conditions, the number of ants collected remained comparatively high, usually due to the dominance of one species. The collections in the PSME/SYAL h.t. in Montana and the ABLA/VAME h.t. in Oregon are exceptions to this trend. The plots in the ABLA/VAME h.t. were located in a cold air drainage where the number of frost free days are usually less than on surrounding slopes. Thus, prolonged periods of

cool temperatures may limit the suitability of this area to many species of ants.

Much fewer species and individual ants were collected in the PSME/SYAL h.t. in Montana compared to that habitat in Oregon. As discussed earlier, the average conditions in this habitat differed between states. In general the plots in Montana had more ponderosa pine than Douglas-fir in the overstory, fewer understory species and lower cover, less woody debris and less accumulated organic matter. Thus the Montana plots represented a more xeric extreme for this habitat type. The greater richness and environmental diversity of the plots in Oregon may also explain why more species and more individual ants were collected there. Whitford and Gentry (1981) working in southern longleaf pine plantations considered the mature stands rather sterile environments and found the greatest number of ant species in newly planted areas where increased understory vegetation and open canopies increased the diversity of the site.

The occurrence of only a few species throughout the range of habitat types is not surprising, considering that as a whole ants are more common in tropical conditions. Several genera, such as Formica, are adapted to temperate zones or have members that are adapted to cooler conditions while the majority of the genus is tropical (eg. Camponotus). The number of species that can survive in boreal and alpine forests is not large, however, due not to a lack of moisture but to fewer frost free days. Researchers who have done extensive collecting in North American coniferous forests have also commented on the monotony of ant species (Gregg 1963, Wheeler 1917).

The 3 Formica species collected commonly in Oregon and Montana are all members of the Formica fusca species group. Although our research (Chapter III) showed that all were predators on western spruce budworm pupae, all were less active predators than either members of the Formica rufa species group or the genus Camponotus. The use of species in the Formica rufa group as biological control agents of forest pests has a long history in Europe (Adlung 1966) and has been investigated in eastern Canada (Finnegan 1971). The F. rufa group is favored over other species groups in the genus because the

workers are large, aggressive, take a wide variety of prey and because colonies are usually very populous. However, our studies show that member of this group are not commonly found throughout the range of habitat types examined in Oregon and Montana. Only 2 species of this group (F. haemorrhoidalis and F. obscuripes) were collected in Oregon, and these were only taken from a total of 3 plots. In general, species of the F. rufa group are found in very open stands, forest meadows, road edges and other areas where the ground receives considerable solar radiation. They are apparently not adapted to closed stands, even within the warm-dry extreme of the moisture-temperature gradients we examined.

Conclusion

Although the species complex varied, ant predators of the western spruce budworm foraged in the canopies of host trees throughout a wide range of forest conditions suitable for the budworm. Absolute numbers of ants collected were low in only 2 types--PSME/SYAL h.t. in Montana and ABLA/VAME h.t. in Oregon--and both represent (although for different reasons) conditions unfavorable for ants. All common ant species were also most active in the canopy during the period when budworm larvae and pupae were present in the foliage (first sample period).

The abundance of all the common species varied considerably among plots over the range of habitat types where they were collected, and the abundance of each species was correlated with a slightly different set of environmental variables. However, in both states, most species were more abundant in less dense stands. Thus it appears that silvicultural manipulations that open up stands would also create conditions more favorable for the colonization of ant predators of the budworm. Reducing stand density is also recommended for silvicultural control of the budworm (Cates and Wulf 1984), and for increasing the suitability of the stands for insectivorous birds that also prey on budworm (Takekawa et al. 1982).

Finally, although members of the Formica rufa species group have been shown to be active budworm predators (Bain 1974, McNeil et al. 1978, Chapter III) their usefulness in the biological control of the western spruce budworm is limited unless stands are greatly manipulated to create conditions favorable to their colonization. It is not likely that the kinds of modifications necessary to promote colonization by members of F. rufa group would be compatible with silvicultural practices in western North America. The abundance of members of the genus Camponotus throughout a range of stand conditions, coupled with the active predation demonstrated by some members (Markin 1979, Chapter III), make this group a more promising subject for further study as possible biological control agents of the western spruce budworm.

Bibliography

- Adlung, K. G. 1966. A critical evaluation of the European research on use of red wood ants (Formica rufa group) for the protection of forests against harmful insects. Z. Angew. Entomol. 57: 167-189.
- Allen, D. C., F. B. Knight, and J. L. Foltz. 1970. Invertebrate predators of the jack-pine budworm, Choristoneura pinus, in Michigan. Ann. Entomol. Soc. Am. 63: 59-64.
- Ayre, G. L. 1959. Food habits of Formica subnitens Creighton (Hymenoptera: Formicidae) at Westbank, British Columbia. Insectes Sociaux 6: 105-114.
- Ayre, G. L. 1963a. Laboratory studies on the feeding habits of seven species of ants (Hymenoptera: Formicidae) in Ontario. Can. Entomol. 95: 712-715.
- Ayre, G. L. 1963b. Feeding behavior and digestion in Camponotus herculeanus (L.) (Hymenoptera: Formicidae). Entomol. exp. appl. 6: 165-170.
- Ayre, G. L. and D. E. Hitchon. 1968. The predation of tent caterpillars, Malacosma americana (Lepidoptera: Lasiocampidae) by ants (Hymenoptera: Formicidae). Can. Entomol. 100: 823-826.
- Bain, O. G. 1974. Two wood ant species attacking western spruce budworm, Choristoneura occidentalis (Lepidoptera: Tortricidae) in western Montana. Unpubl. M.S. Thesis. School of Forestry, University of Montana, Missoula, MT.
- Bernstein, R. and M. Gobbel. 1979. Partitioning of space in communities of ants. J. Anim. Ecol. 48: 931-942.
- Bradley, G. A. 1972. Transplanting Formica obscuripes and Dolichoderus tashenbergi (Hymenoptera: Formicidae) colonies in jack pine stands of southeastern Manitoba. Can. Entomol. 104: 245-249.
- Bradley, G. A. 1973. Interference between nest populations of Formica obscuripes and Dolichoderus tashenbergi (Hymenoptera: Formicidae). Can. Entomol. 105: 1525-1528.
- Bradley, G. A. and J. D. Hinks. 1968. Ants, aphids and jack pine in Manitoba. Can. Entomol. 100: 40-50.
- Campbell, R. W. 1984. Population Dynamics. In M. H. Brookes [ed.], Western Spruce Budworm. U.S. Dept. Agric. Tech. Bull. (in press).
- Campbell, R. W. and T. R. Torgersen. 1982. Some effects of predaceous ants on western spruce budworm pupae in north central Washington. Environ. Entomol. 11: 111-114.

- Campbell, R. W., T. R. Torgersen, and N. Srivastava. 1983. A suggested role for predaceous birds and ants in the population dynamics of the western spruce budworm. *For. Sci.* (in press).
- Cates, R. G. and N. W. Wulf. 1984. Site and Stand Characteristics. In M. H. Brookes [ed.], *Western Spruce Budworm*. U.S. Dept. Agric. Tech. Bull. (in press).
- Cole, A. C. 1942. The Ants of Utah. *Amer. Midl. Nat.* 28: 358-388.
- Cotti, G. 1963. Bibliografia ragionata 1930-1961 del Gruppo Formica rufa in Italiano, Deutsch, English. *Minist. Agric. For. Roma, Coll. Verde* 8. 413 pp.
- Daubenmire, R. and J. B. Daubenmire. 1968. Forest vegetation of eastern Washington and northern Idaho. *Wash. St. Univ. Agric. Exp. Stn. Tech. Bull.* 60. 104 pp.
- David, C. T. and D. L. Wood. 1980. Orientation to trails by a carpenter ant, Camponotus modoc (Hymenoptera: Formicidae). *Can. Entomol.* 112: 993-1000.
- Dixon, A. F. G. 1971a. The role of aphids in wood formation. I. The effect of the sycamore aphid, Drepanosiphon platanoides (Schr.) (Aphididae), on the growth of sycamore, Acer pseudoplatanus (L.). *J. Appl. Ecol.* 8: 165-179.
- Dixon, A. F. G. 1971b. The role of aphids in wood formation. II. The effect of the lime aphid, Eucallipterus tiliae L. (Aphididae), on the growth of the lime, Tilia x vulgaris Hayne. *J. Appl. Ecol.* 8: 393-409.
- Fellin, D. G., R. C. Shearer, and C. E. Carlson. 1983. Western spruce budworm in the northern Rocky Mountains. *N. Wildl.* 9: 2-7.
- Finnegan, R. J. 1971. An appraisal of indigenous ants as limiting agents of forest pests in Quebec. *Can. Entomol.* 103: 1489-1493.
- Finnegan, R. J. 1973. Diurnal foraging activity of Formica sublucida, F. sanguinea subnuda and F. fossiceps (Hymenoptera: Formicidae) in Quebec. *Can. Entomol.* 105: 441-444.
- Finnegan, R. J. 1974. Ants as predators of forest pests. *Entomopnaga* 7: 53-59.
- Finnegan, R. J. 1975. Introduction of a predacious red wood ant Formica lugubris (Hymenoptera: Formicidae) from Italy to eastern Canada. *Can. Entomol.* 107: 1271-1274.
- Finnegan, R. J. 1977. Establishment of a predacious red wood ant Formica obscuripes (Hymenoptera: Formicidae) from Manitoba to eastern Canada. *Can. Entomol.* 109: 1145-1148.

- Finnegan, R. J. 1978. Predation by Formica lugubris (Hymenoptera: Formicidae) on Choristoneura fumiferana (Lepidoptera: Tortricidae). Can. For. Serv. Bi-Mon. Res. Note 34: 3-4.
- Flanders, S. E. 1951. The role of the ant in the biological control of homopterous insects. Can. Entomol. 83: 94-98.
- Fogel, R., M. Ogawa, and J. M. Trappe. 1973. Terrestrial decomposition: A synopsis. Coniferous For. Biome. US/IBP. Rep. 135. 12 pp.
- Fowler, H. G. and R. B. Roberts. 1980. Foraging behavior of the carpenter ant, Camponotus pennsylvanicus, (Hymenoptera: Formicidae) in New Jersey. J. Kans. Entomol. Soc. 53: 295-304.
- Francoeur, A. 1973. Révision taxonomique des especes néarctiques du groupe Fusca, genre Formica (Formicidae, Hymenoptera). Soc. Entomol. du Quebec. Mem. no. 3. 316 pp.
- Franklin, J. F. and C. T. Dyrness. 1973. Natural vegetation of Oregon and Washington. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. PNW-3. 417 pp.
- Gauch, H. G. 1982. Multivariate Analysis in Community Ecology. Cambridge Univ. Press. New York. 298 pp.
- Gösswald, K. 1951. Die rote Waldameise im Dienste der Waldhygiene. Forstwirtschaftliche, Bedeutung, Nutzung, Lebensweise, Zucht, Vermehrung und Schutz. M. Kinau Verlag, Lüneburg. 160 pp.
- Green, G. W. and C. R. Sullivan. 1950. Ants attacking larvae of the forest tent caterpillar, Malacosoma disstria Hbn. (Lepidoptera: Lasiocampidae). Can. Entomol. 82: 194-195.
- Gregg, R. W. 1963. Ants of Colorado. Univ. Colo. Press. Boulder. 792 pp.
- Hall, F. C. 1973. Plant communities of the Blue Mountains in eastern Oregon and southwestern Washington. U.S. Dep. Agric. For. Serv. Reg. 6 Reg. Guide 3-1. 62 pp.
- Hill, M. O. 1979. DECORANA - A FORTRAN program for detrended correspondence analysis and reciprocal averaging. Sect. Ecol. and Syst. Cornell Univ. Ithaca. 52 pp.
- Horstman, K. 1970. Untersuchungen über den Nahrungserwerb der Waldameisen (Formica polyctena Foerster) im Eichenwald. I. Zusammensetzung der Nahrung, Abhängigkeit von Witterungsfaktoren und von der Tageszeit. Oecologia 5: 138-157.

- Horstman, K. 1972. Untersuchungen über den Nahrungserwerb der Waldameisen (Formica polycтена Foerster) im Eichenwald II. Abhängigkeit von Jahresverlauf und von Nahrungsangebot. *Oecologia* 8: 371-390.
- Il'nitzky, S. and J. M. McLeod. 1965. Notes on ants associated with Neodiprion swainei Midd. in jack pine stands in Quebec. *Can. Dep. For. Bi-Mon. Prog. Rep.* 21: 1-2.
- Jennings, D. T. 1971. Ants preying on dislodged jack-pine budworm larvae. *Ann. Entomol. Soc. Am.* 64: 384-385.
- Johnson, C. G. 1982. An interpretation of synecologic relationships in the Billy Meadows area of the Willowa Whitman National Forest. Unpubl. Ph.D. Thesis Dept. Rng. Res. Oreg. St. Univ. 380 pp.
- Krajicek, J., K. Brinkman, and S. Gingrich. 1961. Crown competition - a measure of density. *For. Sci.* 7: 35-42.
- Laine, K. J. and P. Niemela. 1980. The influence of ants on the survival of mountain birches during an Oporinia autumnata (Lep., Geometridae) outbreak. *Oecologia* 47: 39-42.
- Letendre, M., A. Francoeur, R. Béique and J. G. Pilon. 1971. Inventaire des fourmis de la station de biologie de L' Université de Montréal, St. Hippolyte, Quebec. *Natur. Can.* 98: 591-606.
- Majer, J. D. 1976. The ant mosaic in Ghana cocoa farms: further structural consideration. *J. Appl. Ecol.* 13: 145-55.
- Mallis, A. 1941. A list of the ants of California with notes on their habits and distribution. *S. Calif. Acad. Sci. Bull.* 40: 61-96.
- Markin, G. P. 1979. Ants as predators of the western spruce budworm. Paper presented at 1979 Entomol. Soc. Am. annual meeting, Denver, Col.
- Maser, C., R. G. Anderson, K. Cromack, J. T. Williams, and R. W. Martin. 1979. Dead and Down Woody Material, pp 78-95. In J. W. Thomas [ed.], *Wildlife Habitats in Managed Forests - the Blue Mountains of Oregon and Washington*. U.S. Dept. Agric. For. Serv. Agric. Handbook 553.
- Mathers, W. G. 1932. The spruce budworm in British Columbia. *For. Chron.* 8: 154-157.
- McNeil, J. N., J. Delisle, and R. J. Finnegan. 1977. Inventory of aphids on seven conifer species in association with the introduced red wood ant Formica lugubris (Hymenoptera: Formicidae). *Can. Entomol.* 109: 1199-1202.

- McNeil, J. N., J. Delisle, and R. J. Finnegan. 1978. Seasonal predatory activity of the introduced red wood ant, Formica lugubris (Hymenoptera: Formicidae) at Valcartier, Quebec, in 1976. Can. Entomol. 110: 85-90.
- Morris, R. F. 1963. Predation and the spruce budworm, pp 244-243. In R. F. Morris [ed.], The dynamics of epidemic spruce budworm populations. Mem. Entomol. Soc. Can. No. 31.
- Otvos, I. S. 1977. Some parasites and insect predators of the blackheaded budworm in Newfoundland. Can. For. Serv. Bi-Mon. Res. Note 33: 11-12.
- Pavan, M. 1960. Les transplantations de Formica lugubris sur les Apennins de la province de Pavie. Italy Minist. Agric. For. Coll. Verde 7: 161-169.
- Petal, J. 1978. The role of ants in ecosystems, pp 293-325. In M. C. Brian [ed], Production ecology of ants and termites. Cambridge University Press, Cambridge.
- Pfister, R. D., B. L. Kovalchik, S. F. Arno, and R. C. Presby. 1977. Forest Habitat Types of Montana. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. INT-34. 174 pp.
- Post, D. C. and R. L. Jeanne. 1982. Rate of exploitation of arboreal baits by ants in an old-field habitat in Wisconsin. Amer. Midl. Nat. 108: 88-95.
- Price, P. W., C. E. Bouton, P. Gross, B. A. McPheron, J. N. Thompson, and A. E. Weis. 1980. Interactions among three trophic levels: influence of plants on herbivores and natural enemies. Ann. Rev. Ecol. Syst. 11: 41-65.
- Reilly, J. J. and W. L. Sterling. 1983. Dispersion patterns of the red imported fire ant (Hymenoptera: Formicidae), aphids, and some predaceous insects in east Texas cotton fields. Environ. Entomol. 12: 380-385.
- Rosengren, R. 1971. Route fidelity, visual memory and recruitment behavior in foraging wood ants of the genus Formica (Hymenoptera: Formicidae). Acta Zool. Fennica 133: 1-102.
- Sanders, C. J. 1964. The biology of carpenter ants in New Brunswick. Can. Entomol 96: 894-909.
- Sanders, C. J. 1970. The distribution of carpenter ant: colonies in the spruce-fir forests of north-western Ontario. Ecology 51: 865-873.

- Sanders, C. J. 1972. Seasonal and daily activity patterns of carpenter ants (Camponotus spp.) in northwestern Ontario. *Can. Entomol* 104: 1681-1687.
- Silver, G. T. 1960. Notes on a spruce budworm infestation in British Columbia. *For. Chron.* 36: 362-374.
- Skinner, G. J. 1980a. Territory, trail structure, and activity patterns in the wood-ant Formica rufa (Hymenoptera: Formicidae) in limestone woodland in northwest England. *J. Anim. Ecol.* 49: 381-394.
- Skinner, G. J. 1980b. The feeding habits of wood ants Formica rufa (Hymenoptera: Formicidae), in limestone woodland in northwest England. *J. Anim. Ecol.* 49: 417-433.
- Skinner, G. J., and J. B. Whittaker. 1981. An experimental investigation of interrelationships between the wood ant (Formica rufa) and some tree-canopy herbivores. *J. Anim. Ecol.* 50: 313-326.
- Southwood, T. R. E. 1978. *Ecological Methods*. John Wiley and Sons. New York. 524 pp.
- Sudd, J. H., J. M. Douglas, T. Gaynard, D. M. Murray and J. M. Stockdale. 1977. The distribution of wood-ants (Formica lugubris Zelterstedt) in a northern English forest. *Ecol. Entomol.* 2: 301-313.
- Takekawa, J. Y., E. O. Garton, L. A. Langelier. 1982. Biological control of forest insect outbreaks: the use of avian predators. *Trans. 47th N. Amer. Wildlife & Nat. Res. Conf. Wash. D.C.* 1982: 393-409.
- Taylor, L. R. 1961. Aggregation, variance and the mean. *Nature, Lond.* 189: 732-735.
- Taylor, L. R. 1965. A natural law for the spatial disposition of insects. *Proc. XIIth Int. Cong. Entomol.* 1964: 396-397.
- Taylor, L. R., I. P. Woiwod, and J. N. Perry. 1978. The density-dependence of spatial behavior and the rarity of randomness. *J. Anim. Ecol.* 47: 383-406.
- Thomson, H. M. 1957. A note on the predation of spruce budworm pupae. *Can. For. Serv. Bi-Mon. Res. Notes* 13: 2.
- Way, M. J. 1963. Mutualism between ants and honeydew producing Homoptera. *Ann. Rev. Entomol.* 8: 307-344.
- Wellenstein, G. 1980. Auswirkung hügelbauender Waldameisen der Formica rufa - Gruppe auf forstschädliche Raupen und das Wachstum der Waldbäume. *Z. für Ange. Entomol.* 89: 144-157.

- Wheeler, G. C. and J. Wheeler. 1963. The Ants of North Dakota. Univ. N. Dakota. Grand Forks. 326 pp.
- Wheeler, G. C. and J. Wheeler. 1978. Mountain ants of Nevada. Great Basin Nat. 38: 379-396.
- Wheeler, W. M. 1917. The mountain ants of western North America. Proc. Amer. Acad. Arts & Sci. 52: 457-569.
- Whitford, W. G., and J. B. Gentry. 1981. Ant communities of southeastern long leaf pine plantations. Environ. Entomol. 10: 183-185.
- Wilkinson, R. C., A. P. Bhatkar, W. H. Whitcomb, and W. J. Kroft. 1980. Formica integra (Hymenoptera: Formicidae). 3. Trial introduction into Florida. Fla. Entomol. 63: 142-146.

Table II.1 Percent of total ants caught within 0.5 m of the tree trunk on radial boards in each direction in Montana and Oregon in 1981./a

Trial	Direction								Chi ²
	N	NE	E	SE	S	SW	W	NW	
Montana (n=15)	9	20	25	15	17	6	5	3	35.2
Oregon - Trial 1	8	12	13	24	18	9	10	6	19.5
(n=10) Trial 2	10	28	28	9	10	6	3	6	54.5
Trial 3	14	22	24	9	11	8	5	7	27.7

/a Significant differences (P 0.01) among directions in each trial

Table II.2. Correlation between sticky trap catches and average number of ants collected on tree trunks per 3 minute count in Oregon and Idaho in 1981.

Species	Number of trees	Correlation Coefficient
All ants	92	.79
<u>Camponotus modoc</u>	71	.67
<u>C. vicinus</u>	68	.74
<u>C. laevigatus</u>	17	.80
<u>Formica accreta</u>	78	.68
<u>F. podzolica</u>	79	.69
<u>F. neorufibarbis</u>	35	.85

Table II.3. Correlations between sample periods of total ants (by species) caught on traps beneath each of 96 sample trees in Montana and 96 sample trees in Oregon, in 1982.

Ant Species	Montana Sample Periods			Oregon Sample Periods 1-2
	1-2	2-3	1-3	
<u>Camponotus modoc</u>	.94	.97	.83	.81
<u>C. herculeanus</u>	.55	.90	.74	---
<u>C. vicinus</u>	.07	.88	.03	.52
<u>Formica accreta</u>	---	---	---	.75
<u>F. neorufibarbis</u>	.21	.70	.16	.17
<u>F. podzolica</u>	.38	.66	.46	.71

Table II.4. Values of the slope (b), intercept (a) and coefficient of determination (R^2) from Taylor's power law analysis of plot means and variances of ants collected on 24 plots in Montana and 24 plots in Oregon in 1982.

	Montana			Oregon			Montana and Oregon/ ^a		
	a	b	r^2	a	b	r^2	a	b	r^2
<u>Camponotus modoc</u>	3.22	1.99	0.97	1.98	1.89	0.92			
<u>C. herculeanus</u>	3.14	1.87	0.97	--	--	--			
<u>C. vicinus</u>	3.13	1.83	0.99	1.39	1.93	0.89			
<u>Formica accreta</u>	--	--	--	2.45	1.96	0.96			
<u>F. neorufibarbis</u>	2.52	1.72	0.94	2.88	1.83	0.98	2.70	1.81	0.96
<u>F. podzolica</u>	2.69	1.86	0.97	2.22	1.82	0.90	2.54	1.86	0.95

^a/a data from both states pooled if no significant difference ($P < .05$) between state regressions

Table III.1. Plot totals by species of ants caught on sticky traps during 3 days and feeding on budworm during 14, 10-min. observations in 1981 in Oregon.

Plot	<u>Camponotus</u>			<u>Formica</u>				
	<u>vicinus</u>	<u>modoc</u>	<u>laevigatus</u>	<u>accreta</u>	<u>podzolica</u>	<u>neorufibarbis</u>	<u>lasioides</u>	<u>rasilis</u>
Raven								
Sticky trap	306	104	3	436	625	--	3	14
Budworm predator	12	--	1	10	4	--	--	--
Frazier								
Sticky trap	55	74	--	174	237	169	26	--
Budworm predator	1	17	2	--	3	2	1	--

Table III.2. Plot and species totals of ants collected on sticky traps under 10 study trees per plot, over 3 days in 1982 in Oregon and Montana.

Species	Oregon				Montana							Total
	Raven	Frazer	Lower Raven	Starkey	Archibald	Cozy Corners	Camp Utmost	Arkansas Cr.	Lubrecht 1	Lubrecht 2		
<u>Camponotus</u>												
<u>vicinus</u>	153	67	154	72	1	11	34	6	11	8	517	
<u>modoc</u>	33	97	13	81	--	--	--	576	133	1	934	
<u>laevigatus</u>	2	8	3	1	--	--	--	--	--	--	14	
<u>herculeaneus</u>	--	--	--	--	--	--	--	--	17	--	17	
<u>Formica</u>												
<u>accreta</u>	495	139	527	452	2	2	--	--	3	--	1620	
<u>podzolica</u>	593	99	323	336	241	--	50	1736	100	14	3492	
<u>neorufibarbis</u>	2	305	--	86	14	--	--	--	--	--	407	
<u>obscuripes</u>	--	--	--	--	343	606	265	--	19	189	1422	
<u>sp. (microgyna group)</u>	--	--	--	--	--	157	--	--	18	--	175	
<u>lasioides</u>	--	15	5	--	--	--	--	--	--	--	20	
<u>hewitti</u>	--	--	--	--	--	30	--	270	113	--	413	
<u>argentea</u>	12	--	8	--	--	--	--	--	--	--	20	
Total	1290	730	1033	1028	601	806	349	2588	414	212	9051	

Table IV.2. Site characteristics for habitat types in Oregon.

	Habitat Type - PSME/SYAL	ABGR/LIBO - ABGR/VAME	ABLA/VAME
Elevation (m)	1340 - 1435	1275 - 1535	1700 - 1760
Slope	5 - 20°	3 - 15°	5 - 25°
Aspect	SW - NW	N - SW	W - N
Stand age	75 - 90	80 - 120	110 - 180
Tree species	<i>Pseudotsuga menziesii</i> <i>Pinus ponderosa</i>	<i>Pseudotsuga menziesii</i> <i>Abies grandis</i> <i>Pinus contorta</i> <i>Picea engelmannii</i> <i>Larix occidentalis</i>	<i>Pseudotsuga menziesii</i> <i>Abies grandis</i> <i>Abies lasiocarpa</i> <i>Pinus contorta</i> <i>Picea engelmannii</i> <i>Larix occidentalis</i>
Common understory species	<i>Arnica cordifolia</i> <i>Carex geyeri</i> <i>Fragaria</i> spp. <i>Symphoricarpos albus</i>	<i>Arnica cordifolia</i> <i>Adenocaulon bicolor</i> Hook. <i>Chimaphila umbellata</i> <i>Hieracium albiflorum</i> Hook. <i>Linnaea borealis</i> <i>Lonicera utahensis</i> Wats. <i>Osmorhiza chilensis</i> H.&A. <i>Thalictrum occidentale</i>	<i>Arnica cordifolia</i> <i>Cerocarpus ledifolius</i> Nutt. <i>Pyrola</i> spp. <i>Vaccinium membranaceum</i> Dougl. <i>V. scoparium</i>
Soil texture surface/subsurface	sandy - clay loam	loam - silt loam/silt loam	silt loam/loam - silt loam
% gravels-soil	10 - 70	5 - 30	10 - 60

Table IV.1. Site characteristics for habitat types in Montana.

Habitat Type - PSME/SYAL	PSME/VAGL	ABLA/CLUN	ABLA/MEFE
Elevation (m)	1220 - 1325	1575 - 1650	1220 - 1250
Slope	5 - 14°	5 - 14°	0 - 5°
Aspect	SE - SW	SW - NW	---
Stand age	60 - 90	60 - 300	150 - 200
Tree species	Pseudotsuga menziesii Pinus ponderosa	Pseudotsuga menziesii Pinus ponderosa Pinus contorta Larix occidentalis	Pseudotsuga menziesii Pinus contorta Larix occidentalis Abies lasiocarpa Picea engelmannii
Common understory species	Carex geyeri Boott Calamagrostis rubescens Buckl. Spirea betulifolia Pall. Symphoricarpos albus (L.) Blake	Arnica cordifolia Hook. Berberis repens Lindl. Calamagrostis rubescens Carex geyeri Chimaphila umbellata (L.) Bart. Linnaea borealis L. Xerophyllum tenax (Pursh) Nutt. Vaccinium globulare Rydb.	Arnica cordifolia Berberis repens Calamagrostis canadensis (Michx.) Beauv. Clintonia uniflora (Schulf.) Kunth. Chimaphila umbellata Cornus canadensis L. Fragaria spp. Linnaea borealis Smilacina spp. Symphoricarpos albus Thalictrum occidentale Gray Vaccinium caespitosum Michx. V. globulare
Soil texture surface/subsurface	loam/clay - clay loam	loam - silt loam/sandy loam	loam - sandy loam/clay loam or silty - fine sandy alluvium
% gravels-soil	5 - 35	10 - 70	5 - 20
			40 - 60

Table IV.2. Site characteristics for habitat types in Oregon.

	Habitat Type - PSME/SYAL	ABGR/LIBO - ABGR/VAME	ABLA/VAME
Elevation (m)	1340 - 1435	1275 - 1535	1700 - 1760
Slope	5 - 20°	3 - 15°	5 - 25°
Aspect	SW - NW	N - SW	W - N
Stand age	75 - 90	80 - 120	110 - 180
Tree species	<i>Pseudotsuga menziesii</i> <i>Pinus ponderosa</i>	<i>Pseudotsuga menziesii</i> <i>Abies grandis</i> <i>Pinus contorta</i> <i>Picea engelmannii</i> <i>Larix occidentalis</i>	<i>Pseudotsuga menziesii</i> <i>Abies grandis</i> <i>Abies lasiocarpa</i> <i>Pinus contorta</i> <i>Picea engelmannii</i> <i>Larix occidentalis</i>
Common understory species	<i>Arnica cordifolia</i> <i>Carex geyeri</i> <i>Fragaria</i> spp. <i>Symphoricarpos albus</i>	<i>Arnica cordifolia</i> <i>Adenocaulon bicolor</i> Hook. <i>Chimaphila umbellata</i> <i>Hieracium albiflorum</i> Hook. <i>Linnaea borealis</i> <i>Lonicera utahensis</i> Wats. <i>Osmorhiza chilensis</i> H.&A. <i>Thalictrum occidentale</i>	<i>Arnica cordifolia</i> <i>Cerocarpus ledifolius</i> Nutt. <i>Pyrola</i> spp. <i>Vaccinium membranaceum</i> Dougl. <i>V. scoparium</i>
Soil texture surface/subsurface	sandy - clay loam	loam - silt loam/silt loam	silt loam/loam - silt loam
% gravels-soil	10 - 70	5 - 30	10 - 60

Table IV.3. Habitat variables significantly correlated with plot scores on the first two DCA ordination axes of tree and understory vegetation in Montana in 1982.

Habitat Variable	Correlation Coefficient (r)/ <u>a</u>	
	Axis 1	Axis 2
Elevation	-.775	-.489
Slope	-.512	--
Ground Configuration	--	.677
Radiation	.863	--
% Moss	-.482	--
Litter depth	-.689	--
Organic depth	-.817	--
Surface depth	--	-.475
Consistence - surface	.811	--
Consistence - subsurface	.678	--
% gravel - surface		-.552
% gravel - subsurface	.504	-.493
texture - surface		-.514
texture - subsurface	.461	--

/a n = 24, p = .05 when r = .404

Table IV.4. Habitat variables significantly correlated with the abundance of each common Camponotus over all plots and sample periods, and on only those plots where the species was collected in Montana in 1982.

Habitat variables	Correlation coefficient (r)					
	<u>C. vicinus</u>		<u>C. modoc</u>		<u>C. herculeanus</u>	
	All plots/ <u>a</u>	Where collected/ <u>b</u>	All plots/ <u>a</u>	Where collected/ <u>c</u>	All plots/ <u>a</u>	Where collected/ <u>d</u>
Elevation	-.268	---	---	---	.238	---
Radiation	.378	---	---	---	---	---
% Mineral soil	.246	---	---	-.354	.366	.428
Litter depth	-.375	---	---	---	---	---
Stand age	---	---	.351	---	---	---
% Canopy cover	---	---	---	---	-.407	-.436
Snags & stumps	---	---	---	.422	---	---
Organic depth	-.340	---	---	---	---	---
Surface depth	---	---	.300	.590	---	---
Consistence-surface	.339	---	---	---	-.301	-.443
Consistence-subsurface	.311	---	---	---	-.449	---
% gravel-surface	---	---	.337	---	.309	---
% gravel-subsurface	---	---	.304	---	.298	---
texture-subsurface	.394	---	---	---	---	---
<u>7a</u>	n = 72, p = .05 when r = .233					
<u>7b</u>	n = 15, p = .05 when r = .514					
<u>7c</u>	n = 36, p = .05 when r = .329					
<u>7d</u>	n = 39, p = .05 when r = .316					

Table IV.5. χ^2 test of differences in ant abundance between plots with open and closed canopies in Montana in 1982.

Ant Species	Habitat type	No. ants in each canopy class		P
		Open	Closed	
<u>C. vicinus</u>	PSME/SYAL	18	8	<.05
<u>C. modoc</u>	PSME/VAGL	138	105	<.05
<u>C. modoc</u>	ABLA/MEFE	12	1	<.01
<u>C. herculeanus</u>	ABLA/MEFE	217	12	<.005
<u>C. herculeanus</u>	ABLA/CLUN	4	48	<.005
<u>F. podzolica</u>	PSME/SYAL	3	12	<.05
<u>F. podzolica</u>	ABLA/CLUN	241	183	<.01
<u>F. neorufibarbis</u>	PSME/VAGL	38	3	<.005
<u>F. neorufibarbis</u>	ABLA/CLUN	30	37	N.S.
<u>F. neorufibarbis</u>	ABLA/MEFE	111	7	<.005

Mean and Standard Deviation of tree density variables in each density class in each habitat type in Montana in 1982.

Habitat Type	Percent Canopy Cover		Basal Area (m ² /ha)	
	Open	Closed	Open	Closed
PSME/SYAL	83.7 $\pm$ 3.8	90.3 $\pm$ 2.3	23.6 $\pm$ 7.1	36.3 $\pm$ 7.5
PSME/VAGL	81.0 $\pm$ 9.5	93.3 $\pm$ 2.3	23.7 $\pm$ 5.9	41.6 $\pm$ 4.1
ABLA/CLUN	87.7 $\pm$ 5.8	94.7 $\pm$ 3.2	30.5 $\pm$ 6.2	56.5 $\pm$ 2.3
ABLA/MEFE	78.7 $\pm$ 10.4	87.7 $\pm$ 8.4	23.2 $\pm$ 5.7	33.3 $\pm$ 4.6

Table IV.6. Habitat variables significantly correlated with the abundance of each common Formica over all plots and sample periods, and on only those plots where the species was collected in Montana in 1982.

Habitat variables	<u>Correlation coefficient (r)</u>			
	<u>F. podzolica</u>		<u>F. neorufibarbis</u>	
	All plots/ <u>a</u>	Where collected/ <u>b</u>	All plots/ <u>a</u>	Where collected/ <u>c</u>
Elevation	-.243	---	---	---
Slope	-.287	-.532	---	---
Ground configuration	.538	.565	---	---
% Mineral soil	---	---	.278	.405
Stand Age	.354	.402	---	---
% Canopy cover	---	---	-.361	---
Organic depth	---	---	---	-.430
Surface depth	-.580	-.591	---	---
Consistence - subsurface	---	-.507	-.409	-.463
% gravel-surface	-.270	---	---	---
% gravel-subsurface	-.278	---	---	---
Texture-surface	-.549	-.655	---	---
Texture-subsurface	-.373	-.527	---	---

/a n = 72, p = .05 when r = .233

/b n = 30, p = .05 when r = .361

/c n = 36, p = .05 when r = .329

Table IV.7. Habitat variables significantly correlated with plot scores on the first two DCA ordination axes of tree and understory vegetation in Oregon in 1982.

Habitat variable	<u>Correlation Coefficient (r)/a</u>	
	Axis 1	Axis 2
Elevation	-.509	.546
Radiation	.434	-.560
% Mineral soil	.412	---
% Moss	-.438	---
Stand age	-.568	.535
Organic depth	-.523	.463
Surface depth	-.664	-.571
Consistence - surface	.444	---
Consistence - subsurface	---	-.434
% gravel - surface	---	.643

/a $n = 24$, $p = .05$ when $r = .404$

Table IV.8. Habitat variables significantly correlated with the abundance of each common Camponotus over all plots and sample periods, and on only those plots where the species was collected in Oregon in 1982.

Habitat variables	<u>Correlation coefficient (r)</u>			
	<u>C. vicinus</u>		<u>C. modoc</u>	
	All plots/ <u>a</u>	Where collected/ <u>b</u>	All plots/ <u>a</u>	Where collected/ <u>c</u>
Elevation	-.299	-.582	-.299	---
Ground configuration	.317	---	---	---
Radiation	.417	.566	---	---
% Moss	.459	-.523	---	---
Basal area	---	---	-.235	---
CCF	---	---	-.262	---
Organic depth	-.349	---	---	---
Surface depth	-.402	---	---	---
Consistence-surface	.495	.544	---	-.345
Consistence-subsurface	.293	.562	---	---
Texture-surface	.300	.486	---	---
Texture-subsurface	.318	---	---	---

/a n = 48, p = .05 when r = .285

/b n = 18, p = .05 when r = .468

/c n = 34, p = .05 when r = .339

Table IV.9 Chi² test of differences in ant abundance between plots with open or closed canopies in Oregon in 1982.

Ant species	Habitat type	Number of ants in each canopy class		P
		Open	Closed	
<u>C. vicinus</u>	PSME/SYAL	142	122	N.S.
<u>C. modoc</u>	PSME/SYAL	153	36	<.005
<u>C. modoc</u>	ABGR/LIBO/VAME	117	42	<.005
<u>F. accreta</u>	PSME/SYAL	614	225	<.005
<u>F. accreta</u>	ABGR/LIBO/VAME	136	1	<.005
<u>F. neorufibarbis</u>	PSME/SYAL	48	6	<.005
<u>F. neorufibarbis</u>	ABGR/LIBO/VAME	311	37	<.005
<u>F. neorufibarbis</u>	ABLA/VAME	47	22	<.005

Mean and Standard Deviation of tree density variables in each density class in each habitat type in Oregon.

Habitat Type	Percent Canopy Cover		Basal Area (m ² /ha)	
	Open	Closed	Open	Closed
PSME	85.0 ± 2.6	92.8 ± 1.5	28.0 ± 5.5	58.2 ± 15.4
ABGR	74.5 ± 11.2	93.8 ± 4.2	26.6 ± 5.3	49.6 ± 15.8
ABLA	75.3 ± 7.4	89.0 ± 6.1	34.3 ± 11.1	46.6 ± 6.1

Table IV.10 Habitat variables significantly correlated with the abundance of each common Formica over all plots and sample periods, and on only those plots where the species was collected in Oregon in 1982.

Habitat variables	<u>Correlation coefficient (r)</u>					
	<u>F. podzolica</u>		<u>F. acreta</u>		<u>F. neorufibarbis</u>	
	All plots/ <u>a</u>	Where collected/ <u>b</u>	All plots/ <u>a</u>	Where collected/ <u>c</u>	All plots/ <u>a</u>	Where collected/ <u>d</u>
Ground configuration	---	---	.451	.623	---	---
Radiation	---	.584	---	---	---	---
% Mineral soil	---	.761	.406	.492	---	---
% Moss	---	---	---	---	.309	---
Stand age	---	---	-.312	---	---	---
Basal area	.448	.591	---	---	---	---
Organic depth	---	---	-.313	---	---	---
Surface depth	---	---	-.296	---	---	---
Consistence-surface	.454	.657	---	---	---	---
Texture-surface	.570	.613	---	---	---	---
<u>7a</u>	n = 48, p = .05 when r = .285					
<u>7b</u>	n = 12, p = .05 when r = .576					
<u>7c</u>	n = 24, p = .05 when r = .404					
<u>7d</u>	n = 30, p = .05 when r = .361					

Appendix III

Predaceous Ants in Biological Control of Insect Pests of North American Forests

Lorna C. Youngs

Ants are common and usually ignored members of forest communities, yet their activities affect forests in many ways. Their nesting in soil aids soil aeration, movement of soil particles to the surface, accumulation and breakdown of organic matter, and nutrient recycling (Petal 1978). Ants influence vegetation patterns by dispersing seed while foraging, and by creating favorable or unfavorable microhabitats for plant growth near ant mounds. Ant foraging, whether for plant or animal material, can affect both the population dynamics and the distribution of species commonly included in the ants' diet. Although ants feed on a wide range of organic material, my discussion is confined to those ant species that habitually prey on other insects—species that can play an important role in the biological control of forest insect pests.

The development of sociality has enabled ants to interact with their environment in ways unavailable to solitary insects. Group foraging and food sharing supply ant colonies with sufficient resources to support large populations, which in turn, through division of labor, permit the simultaneous performance of all the tasks a solitary insect usually performs sequentially. Ants can modify the microhabitat at the nest site, thus reducing losses of the vulnerable brood stage to environmental stress. The longevity of ant queens and the presence of supplementary reproductives, in many species, confers a kind of immortality on ant colonies. Ant colonies are long-term residents of forest stands.

Research on the Role of Ant Predation in Forest Protection

Research on ant predation on forest pests has been conducted in Europe for well over 100 years (Cotti 1963). This research has concentrated almost exclusively on the mound-building species of the *Formica rufa* group, commonly called red wood ants. This group of species has been singled out because the workers are

large and aggressive, colony populations frequently reach the hundreds of thousands, a wide variety of prey is taken, and colony activity can extend up to 200 days per year in favorable climates (Finnegan 1974). A comprehensive review of the usefulness of ants in European forest protection can be found in Adlung (1966).

Until recently, predaceous ants have received little attention from North American forest entomologists. A few investigators have encountered species of both *Formica* and *Camponotus* feeding on the larvae or pupae of defoliating caterpillars and sawflies, but have not quantified the effects of ant predation on forest pests (Silver 1960, Ilinitzky and McLeod 1965, Bradley and Hinks 1968, Allen et al. 1970, Jennings 1971, Otvos 1977).

Research in the western United States on the population dynamics of the western spruce budworm, *Choristoneura occidentalis* Freeman, has revealed an important role for predaceous ants (Campbell and Torgersen 1982, Campbell et al. 1983). Using exclusion techniques, the investigators measured the predation rates of insectivorous birds, predaceous ants (both *Camponotus* spp. and *Formica* spp.), and both groups on budworm larvae and pupae across a range of budworm densities. At low budworm densities, budworm numbers were 10- to 15-fold greater on trees protected from ant and bird predation, compared with trees accessible to both predator groups. At high budworm densities, protected trees had twice as many budworms as accessible trees. Either birds or ants caused similar budworm mortality in the absence of the other group, and predation by either or both groups was the major source of mortality to the budworm in the late larval and pupal stages (Campbell et al. 1983).

The work of Campbell and Torgersen quantifies the effect of ant predation on budworm survival and thus verifies the earlier investigation of Bain.¹ He found a high rate of budworm larval predation by both *Formica obscuripes* Forel and *F. crinitiventris* Wheeler, although he did not quantify the effect of ant predation on

budworm survival. The conclusions of Campbell et al. (1983) on the importance of ant predation are contrary to those of Markin (1979), who examined the number of budworm larvae and pupae and the amount of defoliation on trees where ants were excluded and on trees routinely foraged by ants. Except at very high ant densities, he found no significant differences between trees, in budworm numbers or defoliation. Because predation by birds was not prevented in his experiments, the compensatory mortality from bird predation demonstrated by Campbell et al. (1983) may have masked differences in budworm mortality between ant-free and ant-foraged trees.

History of the Use of Ants in Biological Control of Forest Pests

European efforts to use ants in biological control of forest pests have concentrated on augmenting native species of the *F. rufa* group. Considerable research has been devoted to methods of quantifying the minimum number of colonies per hectare necessary to promote forest protection and on methods of mass rearing, transplantation, and protection of key ant species (Gosswald 1951). Using the criteria of large aggressive workers, large colony size, colonial nest formation, and multiple queens per colony, researchers have selected *F. polystena* (Foerster) as the primary candidate for augmentation (Cotti 1963). Another species of the *F. rufa* group, *F. lugubris* Zetterstedt, has been augmented to a lesser extent, primarily in alpine forests where *F. polystena* is less common and possibly less successful (Pavan 1960).

In North America, researchers have closely followed European techniques in their attempts to use ants in biological

¹ O. G. Bain. Unpublished report. "Two wood ant species attacking western spruce budworm *Choristoneura occidentalis* (Lepidoptera: Tortricidae) in western Montana." Undated. On file, Pacific Northwest Forest and Range Experiment Station, Corvallis, Oreg. 8 pp.

control of forest pests. In the early 1950s, colonies of three *Formica* species, *F. fusca* L., *F. subnuda* Emery, and *F. integroides* Emery, were transplanted in New Brunswick forests to assess their effects on the spruce budworm, *Choristoneura fumiferana* (Clemens) (Morris 1963). The colonies did not become established, and the experiments were not repeated.

Finnegan (1974), in Quebec, has been a strong supporter of using ants in biological control. Using the European criteria for potentially effective ant species, he (1971) surveyed the indigenous ant fauna of Quebec and concluded that none possessed the necessary characteristics for augmentation programs like those in Europe. Therefore, Finnegan (1975) imported *F. lugubris* from Italy and successfully established colonies in two sites in Quebec. Subsequently, Finnegan (1978) found up to 20% less defoliation by *C. fumiferana* on trees near *F. lugubris* mounds than on distant trees. McNeil et al. (1978) studied the seasonal predatory activity of *F. lugubris* and found that *C. fumiferana* was the most common prey of this ant during peak budworm abundance.

Transplantation of indigenous ant species was attempted later. *Formica obscuripes* colonies were successfully moved from Manitoba into Quebec (Finnegan 1977). Previous work in Manitoba had shown that colonies of *F. obscuripes* could be transplanted from one part of a stand to another (Bradley 1972, 1973).

Attempts to transplant indigenous *Formica* species in the United States have not been successful. Wilkinson et al. (1980) moved *F. integra* Nylander colonies from Georgia into Florida slash pine plantations. Competition between *F. integra* and a local carpenter ant, *Camponotus abdominalis floridanus* (Buckley), resulted in the destruction of the *Formica* colonies. The investigators concluded that, because *C. abdominalis floridanus* dominated the stand and is also predaceous, its potential in biological control should be investigated.

How much forest protection is afforded by ants is still a subject of controversy. Numerous accounts have been published in Europe of red wood ants feeding heavily on defoliating caterpillars and sawflies (e.g., Adlung 1966, Petal 1978), but many studies lack data on the effects of ant predation on pest populations. Some work in England, in hardwood forests, showed a significant reduction in winter moth larvae and their damage, on trees foraged on by red wood ants (Skinner and Whittaker 1981). Red wood

ants were also effective in reducing populations of pine-defoliating caterpillars in southern Sweden (Wellenstein 1980). Studies frequently document the number of insects captured by ant colonies (Horstman 1970, 1972) or the amount of defoliation occurring at various distances from ant mounds (Laine and Niemela 1980).

Possible Disadvantages to Using Ants in Biological Control

Those that question the value of ant predation in the control of forest pests do not deny that ants eat large numbers of pest species. They point out, however, that ants do not feed exclusively on pests. Beneficial insects such as parasitic wasps and flies are included in their diet (Adlung 1966). The impact of ant activity on other beneficial insects is likely to be localized near ant colonies, however, and would depend on the extent that the trees in the area are foraged on by ants, and the extent that ant activity interferes with other beneficial insects.

The tendency for ant colonies to be clumped rather than randomly distributed has supplied critics with an additional reason to question their usefulness in biological control of forest pests. Ants establish foraging territories near their nests, and they are frequently faithful to their foraging routes from year to year (Rosengren 1971, David and Wood 1980). Thus, the scope of their effectiveness may be limited to areas near the nest, producing patches of trees free from insect damage, a so-called "green island" effect (Laine and Niemela 1980). European augmentation programs have been primarily aimed at reducing the degree of patchiness in ant distributions.

The association of many predaceous ants with tree-feeding homopterans has added to the controversy over the benefits of ant predation on forest pests. Honeydew, primarily from aphids, is probably the most widely exploited carbohydrate source of many ant species. The association between ants and aphids has led to various degrees of mutualism (Way 1963). Aphids that allow ants to solicit honeydew frequently increase honeydew production when tended by ants. In turn, ants may provide some degree of protection for the aphids against natural enemies (Flanders 1951).

Aphids tended by ants are often able to maintain higher populations on trees foraged on by ants (Bradley and Hinks 1968, McNeil et al. 1977). High aphid numbers may adversely affect tree growth. Dixon

(1971a,b) found a reduction of sycamore sapling growth and a reduction of root growth in lime samplings associated with high aphid populations. He did not, however, link aphid numbers to the degree of ant tending.

The association of ants with aphids may indirectly benefit forest protection. Honeydew is a fairly stable food source that ant colonies can exploit in periods of low arthropod abundance. Other insect predator-prey systems demonstrate that honeydew provides an alternate food source that sustains predator populations during low prey density (Price et al. 1980).

The effects of aphids cannot be easily evaluated, because detrimental effects on tree growth depend not only on aphid density, but also on the time of feeding and the part of the tree under attack. The relation between ants and aphids can be complex. Aphids themselves may become ant prey (Ayre 1959, Horstman 1970, Skinner 1980), or one aphid species may be protected and another consumed (Skinner and Whittaker 1981). Ant predation on other insects may also be a direct result of aphid protection. Forest tent caterpillars were attacked by *Formica* and *Camponotus* species when larvae ventured too near ant-tended aphid colonies (Green and Sullivan 1950).

The habit of some carpenter ant species of nesting in both living and dead wood may limit the potential use of those species in biological control. Sanders (1964) found three *Camponotus* species infesting live balsam fir and spruce in New Brunswick, and reported an attack rate in New England and the Maritime Provinces of between 0.5 and 4.0% in balsam fir and between 0.5 and 1.0% in spruce. Thus, the degree to which tree-infesting carpenter ant species prey on forest pests would need careful study before their use in biological control could be recommended.

Conclusion

Do predaceous ants have a future in biological control of North American forest pests? European research and augmentation efforts have been extensive, yet even there the verdict is not in. Campbell and Torgersen have shown, for the western spruce budworm, that ant predation is a major mortality factor; this is one of the few instances in North America where the effect of ant predation on the population of a forest insect has been studied in depth. Although McNeil et al. evaluated the predatory activity of the introduced ant species, *Formica lugubris*, very little is known about the native ant species in-

habiting North American forests. The work with western spruce budworm shows that research directed toward quantifying the effects of native ant predation clearly could yield fruitful results. That approach should we take to investigate the potential use of ants in forest protection? Finnegan (1974) has advocated the European approach of colony transplantation and the importation of *Formica rufa* species. The silviculture practiced in European forests is different from that practiced—or, often, not practiced—in North American forests. Centuries of manipulation have created intensely managed European stands, where the augmentation of ant populations by colony transplant or mass releases of laboratory-reared queens is possible. North American forests, especially western forests, are frequently unmanaged, inaccessible, and represent an extremely variable environment. Finding a single *Formica* species comparable to *F. polyctena* in Europe that can be successfully established over such a wide range of conditions is unlikely.

We need much more information about the ant species native to North American forests, their habitat requirements, their geographic distribution, and most important, the degree to which they prey on forest insect pests. From the limited information available for this review, both *Formica* and *Camponotus* apparently contain predaceous species that may have potential for biological control. Many of these species, especially the boreal *Camponotus* species, are found over a range of forest conditions, and their distribution could be extended by augmentation programs. Perhaps a complex of ant species would provide more effective control of forest pests than a single dominant species, and different complexes may be more successful in controlling pests that are widely distributed, such as the spruce budworm. Perhaps also, silvicultural manipulations—such as those that open the stand or create more woody debris for nesting sites—can augment ant populations without costly colony transplantation. But all of these possibilities remain mere speculation until more research is done.

Acknowledgment

I thank David G. Fellin, U.S. Forest Service, Forestry Sciences Laboratory, Missoula, Mont.; Max W. McFadden, U.S. Forest Service, Washington, D.C.; and Daniel B. Twardus, Forest Pest Management, Portland, Oreg., for their review of an earlier draft of this paper.

Work leading to this publication was funded by the USDA Forest Service, Canada/United

States Spruce Budworms Program, Washington, D.C.

References Cited

- Adlung, K. G. 1966. A critical evaluation of the European research on use of red wood ants (*Formica rufa* group) for the protection of forests against harmful insects. *Z. Angew. Entomol.* 57: 167–189.
- Allen, D. C., F. B. Knight, and J. L. Foltz. 1970. Invertebrate predators of the jack-pine budworm, *Choristoneura pinus*, in Michigan. *Ann. Entomol. Soc. Am.* 63: 59–64.
- Ayre, G. L. 1959. Food habits of *Formica subnitens* Creighton (Hymenoptera: Formicidae) at Westbank, British Columbia. *Insectes Sociaux* 6: 105–114.
- Bradley, G. A. 1972. Transplanting *Formica obscuripes* and *Dolichoderus tashenbergi* (Hymenoptera: Formicidae) colonies in jack pine stands of southeastern Manitoba. *Can. Entomol.* 104: 245–249.
1973. Interference between nest populations of *Formica obscuripes* and *Dolichoderus tashenbergi* (Hymenoptera: Formicidae). *Can. Entomol.* 105: 1525–1528.
- Bradley, G. A., and J. D. Hinks. 1968. Ants, aphids and jack pine in Manitoba. *Ibid.* 100: 40–50.
- Campbell, R. W., and T. R. Torgersen. 1982. Some effects of predaceous ants on western spruce budworm pupae in north central Washington. *Environ. Entomol.* 11: 111–114.
- Campbell, R. W., T. R. Torgersen, and N. Srivastava. 1983. A suggested role for predaceous birds and ants in the population dynamics of the western spruce budworm. *For. Sci.* (in press).
- Cotti, G. 1963. *Bibliografia ragionata 1930–1961 del Gruppo Formica rufa in Italiano, Deutsch, English.* Min. Agric. For. Roma, Coll. Verde 8: 413 pp.
- David, C. T., and D. L. Wood. 1980. Orientation to trails by a carpenter ant, *Camponotus modoc* (Hymenoptera: Formicidae). *Can. Entomol.* 112: 993–1000.
- Dixon, A. F. G. 1971a. The role of aphids in wood formation. I. The effect of the sycamore aphid, *Drepanosiphon platanoides* (Schr.) (Aphididae), on the growth of sycamore, *Acer pseudoplatanus* (L.). *J. Appl. Ecol.* 8: 165–179.
- 1971b. The role of aphids in wood formation. II. The effect of the lime aphid, *Eucallipterus tiliae* L. (Aphididae), on the growth of the lime, *Tilia x vulgaris* Hayne. *J. Appl. Ecol.* 8: 393–409.
- Finnegan, R. J. 1971. An appraisal of indigenous ants as limiting agents of forest pests in Quebec. *Can. Entomol.* 103: 1489–1493.
1974. Ants as predators of forest pests. *Entomophaga* 7: 53–59.
1975. Introduction of a predaceous red wood ant *Formica lugubris* (Hymenoptera: Formicidae) from Italy to eastern Canada. *Can. Entomol.* 107: 1271–1274.
1977. Establishment of a predaceous red wood ant *Formica obscuripes* (Hymenoptera: Formicidae) from Manitoba to eastern Canada. *Ibid.* 109: 1145–1148.
1978. Predation by *Formica lugubris* (Hymenoptera: Formicidae) on *Choristoneura fumiferana* (Lepidoptera: Tortricidae). *Bi-Mon. Res. Note* 34: 3–4. [Finnegan, R. J. 1977. Predation of *Choristoneura fumiferana* (Lepidoptera: Tortricidae) par *Formica lugubris* (Hymenoptera: Formicidae). *Rev. Bines. Rech.* 33: 1.]
- Flanders, S. E. 1951. The role of the ant in the biological control of homopterous insects. *Can. Entomol.* 83: 94–98.
- Gösswald, K. 1951. Die rote Waldameise im Dienste der Waldhygiene. *Forstwirtschaftliche, Bedeutung, Nutzung, Lebensweise, Zucht, Vermehrung und Schutz.* M. Kinau Verlag, Lüneberg. 160 pp.
- Green, G. W., and C. R. Sullivan. 1950. Ants attacking larvae of the forest tent caterpillar, *Malacosoma disstria* Hbn. (Lepidoptera: Lasiocampidae). *Can. Entomol.* 82: 194–195.
- Horstman, K. 1970. Untersuchungen über den Nahrungserwerb der Waldameisen (*Formica polyctena* Foerster) im Eichenwald. I. Zusammensetzung der Nahrung, Abhängigkeit von Witterungsfaktoren und von der Tageszeit. *Oecologia* 5: 138–157.
1972. Untersuchungen über den Nahrungserwerb der Waldameisen (*Formica polyctena* Foerster) im Eichenwald. II. Abhängigkeit von Jahresverlauf und von Nahrungangebot. *Ibid.* 8: 371–390.
- Ilnitzky, S., and J. M. McLeod. 1965. Notes on ants associated with *Neodiprion swaini* Midd. in jack pine stands in Quebec. *Can. Dep. For. Bi-Mon. Prog. Rep.* 21: 1–2.
- Jennings, D. T. 1971. Ants preying on dislodged jack-pine budworm larvae. *Ann. Entomol. Soc. Am.* 64: 384–385.
- Laine, K. J., and P. Niemela. 1980. The influence of ants on the survival of mountain birches during an *Oporinia autumnata* (Lep., Geometridae) outbreak. *Oecologia* 47: 39–42.
- Markin, G. P. 1979. Ants as predators of the western spruce budworm. Paper presented at 1979 Entomol. Soc. Am. Annu. Meet., Denver, Colo.
- McNeil, J. N., J. Delisle, and R. J. Finnegan. 1977. Inventory of aphids on seven conifer species in association with the introduced red wood ant *Formica lugubris* (Hymenoptera: Formicidae). *Can. Entomol.* 109: 1199–1202.
1978. Seasonal predatory activity of the introduced red wood ant, *Formica lugubris* (Hymenoptera: Formicidae), at Valcartier, Quebec, in 1976. *Can. Entomol.* 110: 85–90.
- Morris, R. F. 1963. Predation and the spruce budworm. In R. F. Morris [ed.], The dynamics of epidemic spruce budworm populations. *Mem. Entomol. Soc. Can.* No. 31.
- Otvos, L. S. 1977. Some parasites and insect predators of the blackheaded budworm in Newfoundland. *Can. For. Serv. Bi-Mon. Res. Note* 33: 11–12.
- Pavan, M. 1960. Les transplantations de *Formica lugubris* sur les Apennins de la province de Pavie. *Italy Min. Agric. For. Coll. Verde* 7: 161–169.
- Petal, J. 1978. The role of ants in ecosystems. In M. C. Brain [ed.], Production ecology of ants and termites. Cambridge University Press, Cambridge.
- Price, P. W., C. E. Bouton, P. Gross, B. A. McPherson, J. N. Thompson, and A. E. Weis. 1980. Interactions among three trophic levels: influence of plants on herbivores and natural enemies. *Annu. Rev. Syst.* 11: 41–65.
- Rosengren, R. 1971. Route fidelity, visual memory and recruitment behavior in foraging wood ants of the genus *Formica* (Hymenoptera: Formicidae). *Acta Zool. Fenn.* 133: 1–102.

- Sanders, C. J. 1964. *The biology of carpenter ants in New Brunswick*. Can. Entomol. 96: 894-909.
- Silver, G. T. 1960. *Notes on a spruce budworm infestation in British Columbia*. For. Chron. 36: 362-374.
- Skinner, G. J. 1980. *The feeding habits of the wood ant Formica rufa (Hymenoptera: Formicidae) in limestone woodland in north-west England*. J. Anim. Ecol. 49: 417-433.
- Skinner, G. J., and J. B. Whittaker. 1981. *An experimental investigation of interrelationships between the wood ant (Formica rufa) and some tree-canopy herbivores*. J. Anim. Ecol. 50: 313-326.
- Way, M. J. 1963. *Mutualism between ants and boneydew producing Homoptera*. Annu. Rev. Entomol. 8: 307-344.
- Wellenstein, G. 1980. *Auswirkung hügelbauender Waldameisen der Formica rufa-Gruppe auf forstschädliche Raupen und das Wachstum der Waldbäume*. Z. für Ange. Entomol. 89: 144-157.
- Wilkinson, R. C., A. P. Bhatkar, W. H. Whitcomb, and W. J. Kloft. 1980. *Formica integra (Hymenoptera: Formicidae). 3. Trial introduction into Florida*. Fla. Entomol. 63: 142-146.

Note: Received for publication 1 April 1983; accepted 15 August 1983.

Address: Dept. of Entomology, Oregon State University, Corvallis, OR 97331.

Appendix IV

ANTS PREYING ON PUPAE OF THE WESTERN SPRUCE BUDWORM,
CHORISTONEURA OCCIDENTALIS (LEPIDOPTERA: TORTRICIDAE), IN EASTERN
OREGON AND WESTERN MONTANA¹

LORNA C. YOUNGS

Oregon State Department of Agriculture, Salem, Oregon 97310-0110

ROBERT W. CAMPBELL

Forestry Sciences Laboratory, Pacific Northwest Forest and Range Experiment Station
U.S. Department of Agriculture, Forest Service, Corvallis, Oregon 97331

Abstract

Can. Ent. 116: 1665-1669 (1984)

In 1981 and 1982, the following ant species and numbers were detected preying on pupae of the western spruce budworm, *Choristoneura occidentalis* Freeman, in eastern Oregon and western Montana: *Formica obscuripes* Forel, 174; *Camponotus modoc* Wheeler, 160; *C. laevigatus* Smith, 53; *C. vicinus* Mayr, 48; *F. podzolica* Francoeur, 43; *F. accreta* Francoeur, 32; *F. neorufibarbis* Emery, 12; *F. lasioides* Emery, 1; and *Formica* sp. (microgyna group). The *Camponotus* species and *F. obscuripes* were detected preying on budworm on one-third or more of the trees they foraged.

Résumé

En 1981 et 1982, on a trouvé les espèces et nombres suivants de fourmis s'attaquant à la tordeuse occidentale de l'épinette, *Choristoneura occidentalis* Freeman, dans l'est de l'Oregon et l'ouest du Montana: *Formica obscuripes* Forel, 174; *Camponotus modoc* Wheeler, 160; *C. laevigatus* Smith, 53; *C. vicinus* Mayr, 48; *F. podzolica* Francoeur, 43; *F. accreta* Francoeur 32; *F. neorufibarbis* Emery, 12; *F. lasioides* Emery, 1; et *Formica* sp. (groupe microgyna). Les espèces de *Camponotus* ainsi que *F. obscuripes* s'attaquaient à la tordeuse sur le tiers ou plus des arbres sur lesquels elles fourrageaient.

Introduction

Campbell and Torgersen (1982) suggested that predation by ants may be an important factor in the population dynamics of the western spruce budworm, *Choristoneura occidentalis* Freeman, in north-central Washington. Mathers (1932) in British Columbia and Thomson (1957) in Ontario considered ants important budworm predators although they did not identify the species involved. *Formica obscuripes* Forel and *F. criniventris* Wheeler were identified as predators of the western spruce budworm in Montana (Bain 1974). Markin² listed *F. obscuripes*, *F. subnuda* Emery, *F. podzolica* Francoeur, and *F. argentea* Wheeler as possible predators of the western spruce budworm in Idaho.

In eastern North America, efforts have been made to transplant *Formica* species that may prove valuable budworm predators. Colonies of *F. fusca* L., *F. subnuda*, and *F. integroides* Emery were moved to New Brunswick in the early 1950s, but failed to establish (Morris 1963). A European red wood ant, *F. lugubris* Zett., was successfully introduced into Quebec from Italy (Finnegan 1975) and has been observed preying on *C. fumiferana* (Finnegan 1978; McNeil *et al.* 1978).

Ants in the genus *Camponotus* have been identified as possible budworm predators. Sanders (1964) recorded *C. noveboracensis* (Fitch) carrying a *Choristoneura fumiferana* larva, in eastern Canada. Silver (1960) observed many *Camponotus vicinus* Mayr attacking *Choristoneura occidentalis* larvae in British Columbia. Markin found significantly lower *C. occidentalis* pupal densities on trees with large forager populations of *Camponotus herculeanus* (L.).

¹Work leading to this publication was funded by the USDA Forest Service, Canada/United States Spruce Budworms Program, Washington, DC.

²Markin, G. P. 1979. Ants as predators of the western spruce budworm. Paper presented at the Entomological Society of America Annual Meeting, Denver, CO.

In conjunction with a continuing investigation of the role of ant predation in the population dynamics of the budworm, we conducted trials in 1981 and 1982, in eastern Oregon and western Montana, to identify ant species preying on western spruce budworm and to determine the relative importance of the individual species. We identified three *Camponotus* and six *Formica* species predaceous on budworm pupae, and found variation in predation activity among species.

Materials and Methods

1981 trials. The experiments were conducted on two sites on Frazier Mountain in eastern Oregon, in the Union Ranger District of the Wallowa-Whitman National Forest. Both sites had open stands of Douglas-fir, *Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco, and grand fir, *Abies grandis* (Dougl.) Lindl., with mixtures of ponderosa pine, *Pinus ponderosa* Laws.; lodgepole pine, *Pinus contorta* Dougl.; and Engelmann spruce, *Picea engelmannii* Parry.

Twelve open-grown trees of both grand fir and Douglas-fir were selected, six per site. The sample trees ranged from 8 to 18 m in height (avg. 15.5 m) and had abundant ant activity in the foliage and branches easily observable from the ground. All ant species foraging in the tree canopy on each site were represented by the range of species foraging on the sample trees.

Ant predation was observed on stocked budworm pupae. Twigs about 5 cm long bearing pupae were collected from nearby populations and wired to lower crown branch tips of study trees. Each tree was stocked with 30 pupae concentrated on four branches. The pupae on each tree were examined for 10 min every 1.5 h from 0730 h to 1800 h PDT. Pupa at each site were observed on alternate days for a total of 4 days, by which time 70–75% of the pupae were missing. Each pupa not removed was thus observed 14 times. All ants feeding on budworm pupae were collected for later identification.

To determine the ant species foraging on the study trees, ants falling from the trunk and foliage were caught on Tanglefoot®-coated boards. Three boards (0.6 × 0.3 m) were placed around the trunk of each tree, and supported by surveyor's stakes ca. 0.5 m from the ground and 0.25 m from the trunk. In an earlier study, we found that ants frequently fall from the trunk and branches while moving up and down the tree; the rate of falling is proportional to the density of traffic on the trunk. The catch on sticky traps placed close to the trunk is a reliable index of the species composition of ants foraging in the canopy. Sticky traps were placed under each tree at the end of the pupal observation period and left for 3 days.

1982 trials. The experiments were expanded to 10 sites, four in Oregon and six in western Montana. The Oregon sites included the 1981 sites, another site on Frazier Mountain with similar stand characteristics, and a site on the Starkey Experimental Forest dominated by grand fir mixed with Douglas-fir and ponderosa pine. All sites were in the Wallowa-Whitman National Forest.

In Montana, two sites were in the Lubrecht Experimental Forest, 40 km east of Missoula in stands dominated by Douglas-fir mixed with ponderosa pine and western larch, *Larix occidentalis* Nutt. Three sites were on Champion International lands, two near Salmon Lake and the third near Potomac, in mixed stands of Douglas-fir, lodgepole pine, ponderosa pine, and western larch. The sixth Montana site was near Seeley Lake in the Seeley Lake Ranger District of the Lolo National Forest in a mixed stand of Douglas-fir; subalpine fir, *Abies lasiocarpa* (Hook.) Nutt.; ponderosa pine; lodgepole pine; Engelmann spruce; and western larch. Past logging had created open stands in all six sites.

In 1982, ten Douglas-fir trees ranging in height from 1.5 to 25.0 m (avg. 10.3 m) were selected on each plot. The trees were stocked with 20 pupae: 5 per branch on trees taller than 3 m or scattered on branch tips on trees shorter than 3 m. Pupa on each tree

Table I. Number of trees where ant species were detected foraging and collected preying on budworm pupae during fourteen 10-min observations in Oregon, 1981

	Trees* with:				Trees* with:		
	Ants foraging	Ants preying	Total ants		Ants foraging	Ants preying	Total ants
<i>Camponotus</i>				<i>Formica</i>			
<i>laevigatus</i>	3	2	3	<i>accreta</i>	12	5	10
<i>modoc</i>	10	5	17	<i>lasioides</i>	5	1	1
<i>vicinus</i>	11	6	13	<i>neorufibarbis</i>	5	1	2
				<i>podzolica</i>	11	4	7
				<i>rasilis</i>	4	—	—

*Maximum number of trees = 12.

were observed for 5 min on hourly schedules for 3 days after placement. Eight observations were made per day, and the schedule was adjusted to cover the period between 0700 h and 2100 h at least once. Each pupa that was not removed was thus observed 24 times.

Voucher specimens were identified by David Smith, U.S. National Museum, Beltsville, Maryland. The remaining ants were identified by Steven Shattuck, Department of Entomology, Oregon State University, Corvallis, Oregon. All specimens are at the Forestry Science Laboratory, Corvallis, Oregon.

Results and Discussion

Because of differences in experimental design, 1981 and 1982 results are presented separately. In 1981, eight ant species were collected from sticky traps under study trees; seven of these species preyed on budworm (Table I). Although *C. vicinus*, *C. modoc* Wheeler, *Formica accreta* Francoeur, and *F. podzolica* were the most commonly encountered ants on the study trees, relatively more of the *Camponotus* species were collected preying on budworm pupae.

In 1982, twelve ant species foraged on the 100 study trees, an average of seven species per plot in Oregon and five species per plot in Montana (Table II). *Camponotus modoc*,

Table II. Number of trees where ant species were detected foraging and collected preying on western spruce budworm pupae during twenty-four 5-min observations per tree in Oregon and Montana, 1982

	Oregon		Montana		Oregon and Montana		
	Trees* with:		Trees* with:		Trees* with:		Total
	Ants foraging	Ants preying	Ants foraging	Ants preying	Ants foraging	Ants preying	ants preying
<i>Camponotus</i>							
<i>herculeanus</i>	-	-	1	-	1	-	-
<i>laevigatus</i>	8	7	3	3	11	10	50
<i>modoc</i>	29	11	14	3	43	14	143
<i>vicinus</i>	36	13	16	4	52	17	35
<i>Formica</i>							
<i>accreta</i>	37	8	5	3	42	11	22
<i>argentea</i>	3	-	-	-	3	-	-
<i>hewitti</i>	-	-	11	-	11	-	-
<i>lasioides</i>	7	-	-	-	7	-	-
sp. (<i>microgyna</i>)	-	-	4	1	4	1	1
<i>neorufibarbis</i>	14	3	5	1	19	4	10
<i>obscuripes</i>	-	-	37	16	37	16	174
<i>podzolica</i>	32	3	37	13	69	16	36

*a,b,c—Maximum trees 40, 60, and 100, respectively.

C. vicinus, *F. podzolica*, and *F. accreta* were again common in both states. In addition, *F. obscuripes* was prevalent on the Montana plots.

When the number of trees foraged by each species was compared with the number of trees where the species preyed on budworm pupae, the *Camponotus* species, together with *F. obscuripes*, were the dominant predators (Table II). *Camponotus modoc*, *C. laevigatus*, *C. vicinus*, and *F. obscuripes* were collected preying on budworm on one-third or more of the trees they foraged. The number of specimens collected of each species further supports this observation; the *Camponotus* species and *F. obscuripes* represented 85% of all ants observed preying on budworm pupae. *Formica podzolica* and *F. accreta*, although very common species, preyed on budworm on 26% or less of the trees where they occurred and were collected in comparatively low numbers.

We eliminated *F. lasioides* Emery and *Formica* sp. (microgyna group) from consideration as potential budworm predators because they were encountered feeding on budworm only once.

The dominance of *F. obscuripes* among the *Formica* species preying on western spruce budworm is not unexpected. It is the sole representative of the *F. rufa* species group, members of which have been used extensively in European forest protection because of the aggressiveness of the workers and the large populations found in most colonies. *Formica obscuripes* has been considered a possible biological control agent in Canadian forests; it has been transplanted to protect young pine stands in Manitoba (Bradley 1972) and introduced into Quebec (Finnegan 1977). The remaining *Formica* species preying on budworm are from the *F. fusca* group; they are relatively docile, commonly enslaved by other *Formica*.

The predation on budworm exhibited by all of the *Camponotus* species (except *C. herculeanus*, which was found on only one tree) is an indication of a largely unexplored role of this genus as a natural enemy of forest defoliators. Studies focused on foraging activity at the nest or along trails have not found large numbers of insect prey transported to the nest (Sanders 1964, 1972; Fowler and Roberts 1980). Ayre (1963b) suggests that because *Camponotus* workers are unable to ingest solid particles larger than 100 μm , prey may be consumed in the field and transported in the crop as soluble protein and haemolymph. Ayre (1963a) conducted laboratory-feeding studies on *C. herculeanus*; 98% of all live insects offered to the workers were killed and at least partially consumed. Observations of *Camponotus* foraging activity at the site of the prey have given clearer evidence of the predatory behavior of this genus. Green and Sullivan (1950) counted 1800 forest tent caterpillar larvae, *Malacosoma disstria* Hbn., removed by *C. noveboracensis* workers, and Allen *et al.* (1970) listed *C. noveboracensis* among the most common predators of the jack pine budworm, *Choristoneura pinus* Freeman. Otvos (1977) observed *Camponotus herculeanus* feeding on blackheaded budworm, *Acleris variana* (Fern.), larvae.

Conclusion

Species of both *Camponotus* and *Formica* preyed on pupae of the western spruce budworm. The budworm-predator complex was dominated by the *Camponotus* species and *F. obscuripes*, which were detected preying on pupae on relatively more trees in proportion to their occurrence than the remaining *Formica* species. Although any given stocked budworm pupa was observed for only 3 of 48 h in 1981 and 2 of 72 h in 1982, large numbers of ants were observed preying on the pupae.

References

- Allen, D. C., F. B. Knight, and J. L. Foltz. 1970. Invertebrate predators of the jack-pine budworm, *Choristoneura pinus*, in Michigan. *Ann. ent. Soc. Am.* 63: 59-64.
- Ayre, G. L. 1963a. Laboratory studies on the feeding habits of seven species of ants (Hymenoptera: Formicidae) in Ontario. *Can. Ent.* 95: 712-715.

- . 1963b. Feeding behavior and digestion in *Camponotus herculeanus* (L.) (Hymenoptera: Formicidae). *Entomologia exp. appl.* 6: 165–170.
- Bain, O. G. 1974. Two wood ant species attacking western spruce budworm, *Choristoneura occidentalis* (Lepidoptera: Tortricidae), in western Montana. Unpub. M.S. Thesis, School of Forestry, University of Montana, Missoula, MT.
- Bradley, G. A. 1972. Transplanting *Formica obscuripes* and *Dolichoderus taschenbergi* (Hymenoptera: Formicidae) colonies in jack pine stands of southeastern Manitoba. *Can. Ent.* 104: 245–249.
- Campbell, R. W. and T. R. Torgersen. 1982. Some effects of predaceous ants on western spruce budworm pupae in north central Washington. *Environ. Ent.* 11: 111–114.
- Finnegan, R. J. 1975. Introduction of a predacious red wood ant, *Formica lugubris* (Hymenoptera: Formicidae), from Italy to eastern Canada. *Can. Ent.* 107: 1271–1274.
- . 1977. Establishment of a predacious red wood ant, *Formica obscuripes* (Hymenoptera: Formicidae), from Manitoba to eastern Canada. *Can. Ent.* 109: 1145–1148.
- . 1978. Predation by *Formica lugubris* (Hymenoptera: Formicidae) on *Choristoneura fumiferana* (Lepidoptera: Tortricidae). *Can. For. Serv. Bi-Mon. Res. Notes* 34: 3–4.
- Fowler, H. G. and R. B. Roberts. 1980. Foraging behavior of the carpenter ant, *Camponotus pennsylvanicus*, (Hymenoptera: Formicidae) in New Jersey. *J. Kans. ent. Soc.* 53: 295–304.
- Green, G. W. and C. R. Sullivan. 1950. Ants attacking larvae of the forest tent caterpillar, *Malacosoma disstria* Hbn. (Lepidoptera: Lasiocampidae). *Can. Ent.* 82: 194–195.
- Mathers, W. G. 1932. The spruce budworm in British Columbia. *For. Chron.* 8: 154–157.
- McNeil, J. N., J. Delisle, and R. J. Finnegan. 1978. Seasonal predatory activity of the introduced red wood ant, *Formica lugubris* (Hymenoptera: Formicidae) at Valcartier, Quebec in 1976. *Can. Ent.* 110: 85–90.
- Morris, R. F. 1963. Predation and the spruce budworm. pp. 244–248 in R. F. Morris (Ed.), The dynamics of epidemic spruce budworm populations. *Mem. ent. Soc. Can.* 31. 332 pp.
- Otvos, I. S. 1977. Some parasites and insect predators of the blackheaded budworm in Newfoundland. *Can. For. Serv. Bi-Mon. Res. Notes* 33: 11–12.
- Sanders, C. J. 1964. The biology of carpenter ants in New Brunswick. *Can. Ent.* 96: 894–909.
- . 1972. Seasonal and daily activity patterns of carpenter ants (*Camponotus* spp.) in northwestern Ontario (Hymenoptera: Formicidae). *Can. Ent.* 104: 1681–1687.
- Silver, G. T. 1960. Notes on a spruce budworm infestation in British Columbia. *For. Chron.* 36: 362–374.
- Thomson, H. M. 1957. A note on the predation of spruce budworm pupae. *Can. For. Serv. Bi-Mon. Res. Notes* 13: 2.

(Received 8 September 1983; accepted 23 May 1984)

Appendix V

Role of Parasites in the Population Dynamics of the Western Spruce Budworm (Lepidoptera: Tortricidae) in the Northwest

TOROLF R. TORGENSEN, ROBERT W. CAMPBELL,
NILIMA SRIVASTAVA, AND ROY C. BECKWITH

Pacific Northwest Forest and Range Experiment Station, U.S. Department of Agriculture Forest Service,
La Grande, Oregon 97850

Environ. Entomol. 13: 568-573 (1984)

ABSTRACT The relation of parasitization to mortality during the generation (K_c) or from instar IV to adults (K_{L-A}) of western spruce budworm, *Choristoneura occidentalis* Freeman, is examined. Parasitization of budworm larvae and pupae was studied over a wide range of densities (0.3-48.3 larvae per m^2 and 0.1-22.6 pupae per m^2) at sites in Washington, Oregon, Idaho, and Montana. We found that parasites contributed about 9% of the variation affecting generation change, K_c , and about 24% of variation in mortality during the interval from larvae to adults, K_{L-A} .

MUCH EFFORT has been devoted to studying parasites of the western spruce budworm, *Choristoneura occidentalis* Freeman. In the bibliographies of Jennings et al. (1979, 1981) more than 50 citations concern parasites that attack *C. occidentalis*.

A common form of documentation of parasite activity is percent parasitization, or "apparent" parasitism (Miller 1963). Essentially all of the most detailed studies on the parasites of the western spruce budworm have used apparent parasitism as a measure of the relative importance of parasites as a cause of mortality (Wilkes et al. 1948, Carolin and Coulter 1959, Silver 1960, Doganlar and Beirne 1978, Harris and Dawson 1979). McKnight (1971) examined the relation of parasitization to generation- and age-specific survivals in a life table format.

As part of population dynamics studies on the western spruce budworm, we collected detailed information on the parasite complexes associated with this budworm in Washington, Oregon, Montana, and Idaho. The objective of the portion of those studies reported here is to examine the relation of parasitization to variation in budworm survival rates over a range of host densities in these areas.

Materials and Methods

Study Areas. Between 1979 and 1981 we carried out budworm sampling and life table studies at 23 sites in Washington, Oregon, Montana, and Idaho. The five north-central Washington sites were near Winthrop on the east slope of the north Cascades Range and on the Okanogan Highlands near Conconully. Budworm populations throughout this area were generally in a decline phase after a period of high population densities and visible defoliation from 1976 to 1978. The three sites near Winthrop in the Methow River valley were characterized by 10- to 15-m tall Rocky Mountain

Douglas-fir, *Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco, with 3 to 29% of the basal area in ponderosa pine, *Pinus ponderosa* Dougl. ex Laws. The Okanogan Highlands sites were similarly dominated by Douglas-fir, but with a third of the stand basal area represented by overtopping western larch, *Larix occidentalis* Nutt.

We examined four sites in northeastern Oregon on the slopes of the Wallowa Mountains near Union and in the foothills of the Elkhorn Mountains west of Baker. Defoliation was first noticed in this area in 1980. Severity of defoliation continued to increase annually into the 1982 summer season. In the three sites near Union, selective harvests of large overstory trees had left stands composed of Douglas-fir and grand fir, *Abies grandis* (Dougl. ex D. Don) Lindl. These stands also supported mixtures of ponderosa pine; lodgepole pine, *Pinus contorta* Dougl. ex Loud; and Engelmann spruce, *Picea engelmannii* Parry ex Engelmann. The stands west of Baker supported Douglas-fir, grand fir, and ponderosa pine.

Of the 10 sites in Montana, four were near Seeley Lake in the northwestern part of the state on lands administered by Champion International and the USDA Forest Service (Lolo National Forest). Populations were generally increasing in this area. The remaining six sites were west of Butte on the Beaverhead and Deerlodge National Forests. Defoliation was first observed in 1975 in this area. Here, the budworm has produced more severe defoliation continuously from 1979 to 1982. All the Montana sites supported stands dominated by Douglas-fir.

In west-central Idaho we used four sites near McCall that were on either Boise Cascade or Payette National Forest land. All sites had a mixture of full-crown, largely open-grown Douglas-fir and grand fir. On two of the sites Douglas-fir comprised most of the stand; on the other two sites grand fir was the dominant component. In these

sites budworm populations were continuing a 2-year period of light to moderate defoliation.

Budworm populations on either Douglas-fir or grand fir, or both, were sampled. Larval sampling was conducted on 15 sites, two of which had both host tree species (Table 1). Pupal and egg mass sampling was done on all 23 sites, six of which had both hosts (Table 2).

Field and Laboratory Procedures

Tree Selection and Branch Sampling. Sample trees were chosen randomly from among 7- to 14-m trees, or were chosen equally from among 4- to 7-m-, 7- to 14-m-, and >14-m-tall Douglas-fir, grand fir, or both, on 5-ha plots laid out with 0.1-ha grids.

One to three 45-cm terminal tips or whole branches were taken from the middle of each crown third. Branch tips were taken with a pole pruner and basket arrangement (Paul 1979). Whole branches were sampled by a two-person crew with a pole saw and pole pruner. Once a sample branch was chosen, one crew member clamped the branch mainstem with the pole pruner clipperhead, while the other crew member sawed the branch off with the pole saw. Once severed, the branch was gently lowered to a canvas drop cloth.

Branch length was measured from tip to base of the foliage. Branch width was measured from the outermost edge of the foliage on each side, perpendicular to the main stem of the branch. Foliage area of each branch or 45-cm tip was estimated as half the product of the length and the width.

Larval Sampling. Timing of samples at each location was scheduled to coincide with peak occurrence of instar IV. At each plot, 15 to 30 trees per host species were sampled. After sample branches were measured, the foliage was clipped into convenient-sized pieces for examination. In 1979 and 1980, each piece of foliage was held over a drop cloth and rapped vigorously with a stick to dislodge larvae. The foliage was then examined visually for any remaining larvae. In 1981, an alternate method adapted from a technique developed by Martineau and Benoit (1973) was used to dislodge larvae. The technique involved the use of 32-gal (ca. 121-liter) plastic garbage cans. A garbage can, resting on its side at an inclined angle on a wooden stand, was fitted with a coarse wire screen baffle. Foliage was inserted in the can and beaten against the baffle to dislodge the larvae. Larvae were collected from a 1-qt (ca. 0.95-liter) jar mounted through a hole at the lower edge of the can. Repeated examinations determined that further visual checks of the foliage were unnecessary.

A total of 468 whole branches and 2,244 45-cm tips were measured and examined. Density of larvae (N_L) was expressed as number of larvae per m^2 of foliage.

Subsamples of up to five larvae per branch were reared to determine percent parasitization. Larvae were placed individually in plastic petri dishes (7 by 5 cm) supplied with an artificial diet (Robert 1979). Rearing for all stages was conducted at room temperature (20–24°C).

Pupal Sampling. Foliage collections commenced when more than 95% of the adults had emerged and all that remained were pupal exuviae and living, dead, or parasitized pupal remains. Twelve to 30 trees per species per plot were sampled. More than 500 whole branches and 2,618 tips were collected and examined. Foliage was examined visually, and all exuviae, pupae, and other pupal remains were removed, counted, and placed individually in 000 gelatine capsules for rearing. Pupal density (N_{P2}) was expressed as number of pupae, exuviae, and pupal remains per m^2 of foliage.

Egg Mass Sampling. At each plot, 15 to 27 trees per host species were sampled. Egg mass data were obtained from 45-cm tips and linear half-branches. Samples and measurements were done similarly as for larval and pupal samples. After measurements had been made, however, beginning 45 cm back from the terminal tip, the foliage along one side of the main branch was clipped off and discarded. The right- and left-hand sides of the branch were saved alternately. About 4,800 linear half-branches and their 45-cm tips were examined. Needles bearing egg masses were saved in round petri dishes (1 by 5 cm) coded by plot, crown level, and tree species. Subsamples of up to 40 egg masses per plot were extracted to determine egg mass and survival. For each of the 4,154 egg masses examined, we recorded length (mm), number of eggs, length of each row, total number of eggs, number of parasitized eggs, and number of unhatched eggs from all other causes.

When rearings for all stages were terminated, all material was categorized into survival or mortality classes and recorded. Both living and incompletely developed parasites were tallied as successful parasitization. Parasites that had emerged from pupae before collection were assessed on the basis of the emergence hole and on the condition of the interior of the pupa. Parasites were identified, and parasitization was assigned on the basis of the host stage from which the parasite larva, maggot, or adult emerged. Budworm mortality for which cause of death could not be determined was tallied as unknown.

Notation. The number of nominal instar IV per m^2 of foliage is expressed as N_L . Residual pupae (N_{P2}) is the sum of all pupal remains including exuviae per m^2 . Number of adults (N_A) is the number of pupal exuviae per m^2 . N_z is the product of the number of egg masses per m^2 of foliage and mean number of eggs per mass.

Survival of larvae or pupae after the action of parasites, (S_L)_{par} and (S_P)_{par}, respectively, is expressed as:

Table 1. Larval density (N_L) and survival after parasitization, $(S_L)_{par}$, for study sites in various population stages in the Northwest, 1979-1981

Population status and location	Species	Yr	N_L/m^2	No. of larvae sampled	$(S_L)_{par}$
Stable sparse					
New Meadows, Idaho	Douglas-fir	1980	1.7	40	0.90
New Meadows, Idaho	Grand fir	1980	1.8	76	0.87
Archibald, Mont.	Douglas-fir	1981	0.3	19	0.89
Mean					0.80ab
Increasing outbreak					
Arkansas Creek, Mont.	Douglas-fir	1981	5.6	275	0.67
Kozy Korner, Mont.	Douglas-fir	1981	48.3	578	0.88
Raven, Oreg.	Douglas-fir	1981	6.6	673	0.83
Frazier, Oreg.	Grand fir	1981	1.9	382	0.84
Mean					0.81a
Stable outbreak					
Red Ridge, Idaho	Douglas-fir	1980	14.4	141	0.84
Red Ridge, Idaho	Grand fir	1980	25.6	179	0.93
Ponderosa, Idaho	Douglas-fir	1980	8.8	129	0.93
Lardo, Idaho	Grand fir	1980	30.5	185	0.91
Utmost, Mont.	Douglas-fir	1981	23.1	732	0.91
Mean					0.90b
Declining outbreak					
South Salmon Creek, Wash.	Douglas-fir	1979	10.1	54	0.56
B. S. Place, Wash.	Douglas-fir	1979	33.1	771	0.82
Twisp River, Wash.	Douglas-fir	1979	17.2	554	0.78
Robinson Creek, Wash.	Douglas-fir	1979	13.0	349	0.74
Rattlesnake Creek, Wash.	Douglas-fir	1979	13.4	603	0.76
Mean					0.73

Means followed by the same letter are not significantly different.

$$(S_L)_{par} = 1 - \frac{\text{number of larvae parasitized}}{\text{total larvae reared}}$$

$$(S_P)_{par} = 1 - \frac{\text{number of residual pupae parasitized}}{\text{total pupae collected}}$$

Generation survival (S_G) is:

$$\frac{N_A}{N_E} = (S_L)_{par} \cdot (S_P)_{par} \cdot S_{other}$$

where S_{other} is the survival through the generation, after accounting for mortality factors other than parasitization.

Survival from instar IV to adults, S_{L-A} , is:

$$S_{L-A} = (S_L)_{par} \cdot (S_P)_{par} \cdot S_{other}$$

where S_{other} is the survival in the population from instar IV to adults after accounting for mortality factors other than parasitization.

Analyses. Sites were broadly categorized by population status at the time of study, including stable sparse, increasing outbreak, stable outbreak, and declining outbreak. Population status was determined on the basis of forest pest management reports (USDA Forest Service, Annual Reports of Forest Pest Conditions. On file at Portland, Oreg., Boise, Idaho, and Missoula, Mont.) and budworm densities determined by us.

Stage-specific mortalities caused by parasites, other natural enemies, and unknown sources were

expressed in terms of K values. The contribution of each mortality factor to generation change (K_G), or to population change from instar IV to adult (K_{L-A}) were examined in a manner similar to that of Varley and Gradwell (1960), in which:

$$K_G = \log S_G \text{ and } K_{L-A} = \log S_{L-A}$$

Thus, the percent contribution of larval parasitization to K_G and K_{L-A} is expressed, respectively, as:

$$\frac{\log(S_L)_{par}}{\log S_G} \times 100, \text{ and}$$

$$\frac{\log(S_L)_{par}}{\log S_{L-A}} \times 100$$

The percent contribution of pupal parasitization to K_G and K_{L-A} is defined similarly.

Chi-square tests with Yates correction were used to compare parasitization between populations in the assigned population categories listed above. Comparisons of the contributions of parasitization and unknown or unidentified mortalities to variation in survival were made using variance-covariance matrix analysis (Mott 1966). Combined data from all sites for 1979-1981, and from both tree species (Tables 1 and 2) were used to construct matrices for survival from instar IV to adult (S_{L-A}) and for generation survival (S_G).

Table 2. Pupal density (N_p) and survival after parasitization, (S_p), at study sites in various population stages in the Northwest; 1979-1981

Location	Species	Yr	N_p	No. of pupae sampled	(S_p)
Stable sparse					
New Meadows, Idaho	Douglas-fir	1980	0.1	29	0.97
New Meadows, Idaho	Grand fir	1980	0.1	34	0.97
Archibald, Mont.	Douglas-fir	1981	0.02	10	0.70
Mean					0.88a
Increasing outbreak					
Arkansas Creek, Mont.	Douglas-fir	1981	0.9	99	0.86
Kozy Korner, Mont.	Douglas-fir	1981	11.3	1,340	0.76
Raven, Oreg.	Douglas-fir	1981	0.8	115	0.94
Raven, Oreg.	Grand fir	1981	1.4	67	0.93
Frazier, Oreg.	Douglas-fir	1981	0.3	50	0.95
Frazier, Oreg.	Grand fir	1981	0.1	72	0.95
Marble Creek, Oreg.	Douglas-fir	1981	10.3	677	0.87
Marble Creek, Oreg.	Grand fir	1981	14.7	581	0.85
Mean					0.89a
Stable outbreak					
Red Ridge, Idaho	Douglas-fir	1980	7.7	261	0.93
Red Ridge, Idaho	Douglas-fir	1981	5.8	154	0.84
Red Ridge, Idaho	Grand fir	1980	7.5	788	0.94
Red Ridge, Idaho	Grand fir	1981	5.0	208	1.00
Ponderosa, Idaho	Douglas-fir	1980	3.9	617	0.97
Lardo, Idaho	Grand fir	1980	9.8	906	0.93
Lardo, Idaho	Grand fir	1981	11.3	442	0.95
Utmoot, Mont.	Douglas-fir	1981	7.2	1,188	0.92
Pigeon Creek, Mont.	Douglas-fir	1981	4.0	303	0.88
Toll Canyon, Mont.	Douglas-fir	1981	6.0	327	0.82
Fleecer, Mont.	Douglas-fir	1981	6.7	421	0.87
Crazy Swede Creek, Mont.	Douglas-fir	1981	7.2	352	0.81
Jimmy New Creek, Mont.	Douglas-fir	1981	22.6	460	0.67
Jerry Creek, Mont.	Douglas-fir	1981	8.2	355	0.86
Mean					0.89a
Declining outbreak					
B. S. Place, Wash.	Douglas-fir	1979	19.3	228	0.60
Twisp River, Wash.	Douglas-fir	1979	4.3	60	0.80
Robinson Creek, Wash.	Douglas-fir	1979	4.2	51	0.41
Rattlesnake Creek, Wash.	Douglas-fir	1979	4.7	70	0.60
Cove, Oreg.	Douglas-fir	1981	9.9	371	0.73
Cove, Oreg.	Grand fir	1981	6.8	320	0.75
Mean					0.63

Means followed by the same letter are not significantly different.

Results

Egg Mass Density, Number of Eggs, and Parasitization. Egg mass density varied from <1 to 70 per m^2 . There was a mean of 47.5 ± 10.6 eggs per mass. Parasitization was generally low, averaging only $1.2 \pm 0.5\%$.

Larval Density and Parasitization. Instar IV densities (N_L) varied from about 0.3 to 48.3 (mean = 15.0 ± 3.2), with most of the observations (11 of 17) being between 1.7 and 17.2 per m^2 . Within this range of host densities apparent parasitization varied from 7 to 44%, with 12 of 17 observations falling between 7 and 18% (mean = 17.0 ± 2.4). Parasitization was determined from collections totalling 5,740 larvae, or 19 to 771 (mean = 241) larvae per site (Table 1).

Group means for larval parasitization differed significantly ($P = <0.001$) among all three groups of outbreak status populations; increasing, stable,

and decreasing outbreaks. Parasite activity in stable sparse populations did not differ significantly from areas with increasing or stable outbreaks, but it was much lower than parasitization in the declining outbreaks ($P = <0.001$).

Pupal Density and Parasitization. Density of residual pupae (N_p) varied between 0.03 and 22.6 per m^2 , with 28 of 31 observations falling below 11.3 (mean = 6.5 ± 1.0) per m^2 . Apparent parasitization was 0 to 59% (mean = 16.0 ± 2.5), based on 10,845 pupae, or 10 to 906 (mean = 350) pupae per site (Table 2).

Group means for pupal parasitization among populations categorized as stable sparse, or as increasing or stable outbreaks did not differ. However, the means for each of these groups were significantly lower than the mean for declining outbreaks ($P = <0.001$).

Contributions of Parasitization to Mortality.

Table 3. Percent contribution of larval (L_{par}) and pupal parasitization (P_{par}) to variation in generation survival (K_G) and survival from instar IV to adults (K_{L-A}) at selected western budworm study sites

Population status	Mean % of K_G contributed by:			Mean % of K_{L-A} contributed by:		
	L_{par}	P_{par}	Other	L_{par}	P_{par}	Other
Stable sparse	2.0	2.7	95.3	4.0	4.7	91.3
Increasing outbreak	5.3	3.0	91.7	8.8	6.3	84.9
Stable outbreak	3.2	1.8	95.0	11.2	6.2	82.6
Declining outbreak	5.7	13.2	81.0	18.0	30.2	51.8
Mean of all sites	4.0 ± 0.15	5.1 ± 0.04	90.8 ± 1.78	11.3 ± 0.43	13.1 ± 0.90	76.3 ± 4.63

From instar IV (L) to adults (A), mean larval and pupal parasitization (L_{par} and P_{par}) for all areas combined accounted for about 24% of K for the interval. Parasites from both larvae and pupae contributed about equally to K (11 vs. 13%), but the range in percentage contribution by pupal parasitization among categories (4–30%) was greater than for larval parasitization (4–18%). The mean contribution of all parasites to generation K (K_G) for all areas combined was about 9%, and was also about equally divided between larval and pupal parasites. The range in percent contribution of L_{par} and P_{par} to K was about 2 to 6 and 2 to 13, respectively.

Among the stable sparse populations, larval and pupal parasitization (L_{par} and P_{par}) contributed about equally to K . Among increasing and stable outbreak populations, larval parasitization (L_{par}) was the dominant contributor to variation in both K_G and K_{L-A} . Declining outbreak populations were more influenced by pupal parasites (P_{par}). Mortality factors other than L_{par} and P_{par} accounted for 81 to 95% (mean = 91%) of the variation in K_G (Table 3).

Variance-Covariance Matrix. The matrices in Table 4 a and b show the contribution of (S_L) $_{par}$ and (S_P) $_{par}$ to both S_{L-A} and S_G , respectively, among all areas combined. Both matrices show that the contributions of parasitization to variation in bud-

worm survival is low. Other sources of mortality, S_{other} , are, therefore, dominant contributors of variation in both S_{L-A} and S_G . The presence of the negative covariance terms shared between S_{other} and both (S_L) $_{par}$ and (S_P) $_{par}$ tends to reinforce the major contribution of S_{other} to variation in budworm survival.

Parasite Species Obtained. Fourteen species of parasites were consistently represented in the rearings. The species, listed in approximate order of decreasing dominance—*Apanteles fumiferanae* Viereck, *Glypta fumiferanae* (Viereck), *Chorion gracile* (Provancher), *Enytus montanus* (Ashmead), and *Mesochorus tachypus* Holmgren (a secondary parasite)—were all from larvae. Species reared from pupae were: *Agria housei* Shewell, *Madremyia saundersii* (Williston), *Ceromastix auricaudata* Townsend, *Phaeogenes maculicornis hartioli* (Cresson), *Itoplectis quadricingulata* (Provancher), *Ephialtes ontario* (Cresson), *Phorocera incrassata* Smith, and *Timavia fumiferanae* (Tothill). *Trichogramma minutum* (Riley) was the only parasite reared from budworm eggs.

Discussion

Within the wide range of larval and pupal densities we observed, parasitization varied widely, too, from 0 to 59% (Tables 1 and 2). Means for larval and pupal parasitization by area, representing both increasing and decreasing budworm populations, varied almost as much, from 5 to 43%.

Conventional logic would suggest that high parasitization—more than ca. 15%—should be important, and should show a reasonably clear relation to budworm trend. The contribution of L_{par} and P_{par} to K_{L-A} was ca. 15% for the increasing outbreak sites in Oregon and Montana. Thus, even where parasitization was rather high, budworm populations were still increasing. In Washington, where parasites contributed ca. 48% of the variation in K_{L-A} (ca. 19% to K_G), the population had been decreasing for several years. This suggests that parasites may play an active role in regulating declining populations, or it indicates that parasites are merely exploiting already diminishing numbers of hosts and thereby reinforcing the population collapse.

In studies designed to examine the role of insectivorous birds and foliage foraging ants on budworm numbers, we found that birds and ants, or

Table 4. Components of variance and covariance in observed survival from (A) instar IV to adults (S_{L-A}) and (B) for the entire generation (S_G) due to activity of larval and pupal parasites (L_{par} and P_{par} , respectively), and other sources (S_{other}), expressed as percentages of total variance; pooled data from all sites, 1979–1981

A. Source	(S_L) $_{par}$	(S_P) $_{par}$	S_{other}	S_{L-A}
(S_L) $_{par}$	0.89	1.0	-2.3	-0.4
(S_P) $_{par}$	—	5.8	-5.9	trace
S_{other}	—	—	107.8	99.6
S_{L-A}	—	—	—	100.0
(n = 17)				
B. Source	(S_L) $_{par}$	(S_P) $_{par}$	S_{other}	S_G
(S_L) $_{par}$	2.7	1.5	-1.4	2.8
(S_P) $_{par}$	—	9.6	-14.5	-3.4
S_{other}	—	—	116.4	100.4
S_G	—	—	—	100.0
(n = 16)				

All sites and both host tree species in Tables 1 and 2 were used in constructing the matrix for S_{L-A} ; South Salmon Creek was omitted from the matrix for S_G .

either predator guild alone, contributed about 29% of the variation in K_c . When both predator guilds were excluded from budworm populations on 9-m-tall trees (Campbell et al. 1981), all the other mortality factors, including parasites and other predators, contributed relatively little to mortality. More significantly, these "other" unknown mortalities were not capable of compensating for the absence of the predator guilds by increasing their own activity, at least not within the generation (Campbell and Torgersen 1983, Campbell et al. 1983).

Our studies show that, overall, parasitization contributed very little to variation in either S_{L-A} or S_c in the sites we examined (Table 4), and that parasites are apparently slow to respond to increases in available hosts. We believe these data indicate that, for the various host densities we observed over a large portion of the insect's range, parasites may have a lesser role in the population dynamics of the western spruce budworm than previously thought. Although the contribution to population regulation by parasites alone is not impressive, the composite effects of parasitization and predation by birds and ants make it clear that these guilds should be adequately considered in the choice of chemicals for suppression of western spruce budworm. In particular, it is imperative that only formulations that have minimal effects on hymenopterans, dipterans, and insectivorous birds be used.

Acknowledgment

We express our heartfelt thanks to K. P. Hosman for supervising field personnel and for technical laboratory assistance, and to the field crews who worked on this study. We thank D. T. Jennings, J. M. Schmid, A. J. Thomson, W. J. A. Volney, and C. B. Williams, who reviewed an earlier draft of this manuscript. This study was funded in part by the CANUSA Spruce Budworms Program, Portland, Oreg.

References Cited

- Campbell, R. W., and T. R. Torgersen. 1983. Compensatory mortality in defoliator population dynamics. *Environ. Entomol.* 12: 630-632.
- Campbell, R. W., T. R. Torgersen, S. C. Forrest, and L. C. Youngs. 1981. Bird exclosures for branches and whole trees. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. PNW 125.
- Campbell, R. W., T. R. Torgersen, and N. Srivastava. 1983. A suggested role for predaceous birds and ants in the population dynamics of the western spruce budworm. *For. Sci.* 29: 779-790.
- Carolin, V. M., and W. K. Coulter. 1959. The currence of insect parasites of *Choristoneura fumiferana* (Clem.) in Oregon. *J. Econ. Entomol.* 52: 555.
- Doganlar, M., and B. P. Beirne. 1978. Natural enemies of budworms, *Choristoneura* spp. (Lepidoptera: Tortricidae), on Douglas-fir near Yale, British Columbia, in 1977. *J. Entomol. Soc. B.C.* 75: 25-26.
- Harris, J. W. E., and A. F. Dawson. 1979. Parasitoids of the western spruce budworm, *Choristoneura occidentalis* (Lepidoptera: Tortricidae), in British Columbia 1977-78. *Ibid.* 76: 30-38.
- Jennings, D. T., S. C. Hacker, F. B. Knight, and M. E. McKnight. 1981. Spruce budworms bibliography. Supplement 1. Maine Life Sci. Agric. Exp. Stn. Misc. Rep. 255.
- Jennings, D. T., F. B. Knight, S. C. Hacker, and M. E. McKnight. 1979. Spruce budworms bibliography. Maine Life Sci. Agric. Exp. Stn. Misc. Rep. 213.
- Martineau, R., and P. Benoit. 1973. A sampling technique for estimating numerical trends in larval populations of insect defoliators on conifers. II. Modification and operational use of the technique for extensive sampling of spruce budworm populations in Quebec. *Phytoprotection* 54: 23-31.
- McKnight, M. E. 1971. Natural mortality of the western spruce budworm, *Choristoneura occidentalis* in Colorado. U.S. Dep. Agric. For. Serv. Res. Pap. RM-81.
- Miller, C. A. 1963. Parasites and the spruce budworm, pp. 228-241. In *The dynamics of epidemic spruce budworm populations*. Mem. Entomol. Soc. Can. 31.
- Mott, D. G. 1966. The analysis of determination in population systems, pp. 179-194. In K. E. F. (ed.), *Systems analysis in ecology*. Academic Inc., New York.
- Paul, H. G. 1979. How to construct larval sampling equipment. U.S. Dep. Agric. For. Serv. Agric. Handb. 545. Washington, D.C.
- Robertson, J. L. 1979. Rearing the western spruce budworm. Can. U.S. Spruce Budworms Program, U.S. Dep. Agric. For. Serv., Washington, D.C.
- Silver, G. T. 1960. Notes on a spruce budworm infestation in British Columbia. *For. Chron.* 36: 362-374.
- Varley, G. C., and G. R. Gradwell. 1960. Key factors in population studies. *J. Anim. Ecol.* 29: 399-401.
- Wilkes, A., H. C. Coppel, and W. G. Mathers. 1948. Notes on the insect parasites of the spruce budworm *Choristoneura fumiferana* (Clem.) in British Columbia. *Can. Entomol.* 80: 138-155.

Received for publication 19 May 1983; accepted 21 December 1983.

Appendix VI

DOCUMENT HEADER

Document name: HeadCap Codes&Procedures Document type: WRD

Drawer: SCHMIDT

Folder: HeadCap Codes&Procedures

Last modified on 29 May,86

14:10

by F.SCHMIDT

Author: FRED H. SCHMIDT

Typist: FRED H. SCHMIDT

Subject: SBW Larval Head Capsule File Codes & Procedures

Summary:

The following describes the code assignments used in naming all files created for SBW head capsule width data, including Plot codes, other collection information, measurement procedures, and the 'Schmidt' head capsule and prothoracic plate Color Code System.

Comments:

SBW Larval Head Capsule File Codes and Procedures

Generalized Form of File Codes: LLHZPZ.DTX

Where: LL = Plot Code

H = Head Capsule

P = Prothoracic Shield (= Prothoracic Plate, = Plate)

Z = Color Code Value [1 (lightest), 3, or 6 (darkest)] [Schmidt modification of scheme developed by Harvey and Stehr 1967. (Harvey, G. T., G. Stehr 1967. *Can. Ent.* **99**: 464-481. "On coniferophagous species of *Choristoneura* (Lepidoptera: Tortricidae) in North America. III. Some characters of immature forms helpful in the identification of species." (re. p.466ff)].

D = Last Numeral of Collection Year (eg. 3 = 1983).

T = Tree Host (D = Douglas-fir, G = Grand Fir, W = White Fir, & Y = all hosts on plot).

X = Collection Date Series (1 = First collection in collection year, 2 = Second collection in year, etc. X = Sum of all collections in year).

Plot Codes (Numerical order): Plot-

<u>No.</u>	<u>Alpha</u>	<u>Name and Location</u>
01	UT	Camp Utmost, Montana
02	AR	Archibald Loop, Montana
03	AK	Arkansas Creek, Montana
04	KK	Kozy Korners, Montana
10	CT	Cove (Thinned) [Mill Creek], Oregon
11	CU	Cove (Unthinned) [Mill Creek], Oregon
12 or 13	ST	Starkey (Bally Mountain), Oregon
21	RV	Raven, Oregon
22	FR	Frazier (Mountain or) Lookout, Oregon
27	DC	Dan's Creek (John Day), Oregon
28	MC	Murderer's Creek (John Day), Oregon
29	SR	Starr Ridge (John Day), Oregon
30	HS	Herberger Spring (John Day), Oregon
33	RR	Red Ridge, Idaho
35	LR	Lardo, Idaho
40	F1	Fenton Hill-1 (Jemez Springs), New Mexico
41	F2	Fenton Hill-2 (Jemez Springs), New Mexico
42	BR	Bruce Ridge (Jemez Springs), New Mexico
43	CP	Cerro Pelado (Jemez Springs), New Mexico

Collection Preservative: KAAD (usually, unless otherwise specified)

K = Kerosene (1 part)

A = Ethyl Alcohol, 95% (7 parts)

A = Glacial Acetic Acid (1 part)

D = Dioxane (1 part)

Head Capsule Width Measurements:

- Apparatus - Dendrochronometer, Apple II-Plus Computer, & Tree Ring Program.
- Measurement Units - 0.1 mm X 10, so the output from the tree ring program must be divided by 10 in order to obtain a "true" metric equivalent (in mm).
- Measurements - Made to the nearest 0.05 mm.

HZPZ.4Y2	WRD
HZPZ.4YB	WRD
HZPZ.4YX	WRD
F2HZPZ.4Y1	WRD
F2HZPZ.4Y2	WRD
F2HZPZ.4YX	WRD

Folder: 84 ORE SBW HEAD CAPSULES

Folder: 85 ORE SBW HEAD CAPSULES

DCHZPZ.5DX	WRD
DCHZPZ.5GX	WRD
DCHZPZ.5YX	WRD
HSZPZ.5DX	WRD
HSZPZ.5GX	WRD
HSZPZ.5YX	WRD
MCHZPZ.5DX	WRD
MCHZPZ.5GX	WRD
MCHZPZ.5YX	WRD
SRHZPZ.5DX	WRD
SRHZPZ.5GX	WRD
SRHZPZ.5YX	WRD

Folder: BATCH NORMAL DESCRIPTION

BATCH NORMAL	WRD
BATCH-NORMAL	WRD
NORMAL-CIMON	WRD

Folder: HeadCap Codes&Procedures

HeadCap Codes&Procedures WRD

Folder: Normal Programs

NORMAL.CLI	WRD
NORMAL.F77	WRD

-----X-----

Appendix VII

Chapter 6

Population Dynamics

① 6.1 Introduction

Robert W. Campbell

② 6.1.1 Likelihood and Persistence of Outbreaks

Throughout its range, detectable populations of the western budworm appear to persist indefinitely in stands that contain a substantial proportion of suitable hosts. Populations in these stands have exhibited one of three numerical patterns. The first pattern, chronically high populations, occurs in many stands, particularly in Montana and Idaho. In one extreme case, visible defoliation was recorded for 29 successive years in the same stand. Thirteen of 91 documented outbreaks (14 percent) persisted without a break for at least 9 years; 32 of 91 (35 percent) persisted for at least 4 years (Johnson and Denton 1975). In the second pattern, outbreaks may only last for 1 or 2 years. Even in the northern Rocky Mountain area reported by Johnson and Denton (1975), 44 of 91 outbreaks (48 percent) persisted for only 1 or 2 years.

Persistence at sparse densities is the third numerical pattern exhibited by the budworm. Unfortunately, only a few records document this sparse pattern. Unlike outbreaks, which are obvious, sparse populations are only detectable by sampling.

2
6.1.2 Outbreaks ^{and} ~~Weather~~ Weather

Several investigators have found correlations between warm, dry periods and subsequent outbreaks in both the eastern and western budworms. Hard and others (1980) examined records from northwest Montana and northern Idaho. They found that defoliation varied with weather during May, June, and July of the previous year $\frac{1}{m}$ directly with mean maximum temperature and inversely with the frequency of days with measurable precipitation. Similarly, Twardus (1980 unpubl.) found in north-central Washington that warm, dry periods often preceded outbreaks. In British Columbia, Thomson and others (1984) found that synchrony of larval emergence and budburst $\frac{1}{m}$ also dependent on weather factors $\frac{1}{m}$ were associated with the weather of the preceding year. The collapse of two of the five outbreaks studied was clearly associated with extreme high temperatures after moth flights.

Blais (1957, 1968) associated eastern budworm infestations with dry summers and suitable densities of host species.

6-1A
From defoliation records, Kemp and others (1983 unpubl.) defined three broad classes of outbreak frequency in the forested areas of four States (fig. 6-1, bottom). They examined several climatic features in Washington, Oregon, Idaho, and Montana to determine their association with budworm outbreaks. They concluded that outbreaks were associated with drier climates, and that outbreaks occur most often in a fairly

limited range of mean temperatures in January and July. Generally, outbreaks occurred where annual precipitation was between 9 and 36 inches (23 and 91 cm). Outbreaks were also associated with January and July temperatures:

	Mean		Mean	
	minimum		maximum	
	<u>°F</u>	<u>°C</u>	<u>°F</u>	<u>°C</u>
January	3 to 23	-16 to -5	26 to 38	-3 to 3
July	40 to 53	4 to 12	75 to 90	24 to 32

Links between climatic trends and defoliation frequency remain somewhat obscure. Kemp and others speculated that this linkage may be through increased host-plant stress and increased insect survival. They did not analyze weather trends that might be associated with the end of an outbreak. Once a population is released, adverse physical factors^l such as cold, wet summers^l may not bring either the eastern or western budworm under control (Greenbank 1956, Thomson and others 1983 unpubl.).

Using procedures similar to Kemp's, Van Sickle (personal communication) provided an outbreak frequency map of British Columbia (fig. 6-1, top). Note that the zones of outbreak frequency are defined differently in the two areas; in British Columbia, outbreaks were shorter, fewer, or both.

① 6.2 Overall Numerical Behavior

Fellin and others (1983) summarized the history of the western budworm in the northern Rocky Mountains as follows:

Two infestations were reported near Priest Lake in northern Idaho [in 1922]. Over the next 30 years, only scattered and insignificant infestations were reported. . . . The first significant outbreak . . . began about 1948 and has persisted until now [1983].

Over Western North America, budworm densities may range over five orders of magnitude. Populations are usually either at densities where they are barely discernible by standard sampling techniques, or at densities so high that defoliation is obvious. Populations of intermediate density are in transition^I_M—either increasing to outbreak, or decreasing to sparse. The significance of this pattern is that it focuses attention on the two major population modes (outbreak and sparse) and two transient phases (release and decline) where we must have information for evaluating and understanding numerical changes. Processes that appear to dominate each mode or phase of this life system (sparse, release, outbreak, and decline) are summarized below.

② 6.2.1 Sparse Mode

Populations may be considered sparse if their average density is less than one egg mass (20 to 50⁺ eggs) per square meter of foliage. Poor survival is characteristic from fourth instar to residual pupae (pupae remaining after predation) among sparse, stable populations (6.6.1). At least in the Northwestern United States, this low survival is established largely through predation by birds and ants (6.6.3). Unless unusually high survival or inward migration occurs during other stages, this predation appears adequate to maintain populations at sparse densities indefinitely.

Egg?

② 6.2.2 Release Phase

Two major events, either singly or together, are sufficient to enable a sparse population to increase to an outbreak: high survival during dispersal (fall and spring) of small larvae (6.4.5); and redistribution of egg masses by gravid females (6.7).

High survival during larval dispersal is associated with abundant host foliage, multistoried stands, and a particularly favorable conjunction between spring budburst and emergence of the larvae from hibernation. Relatively little is known about the redistribution of eggs by adult females, but the adult insects appear particularly likely to lay their eggs in the tops of older trees (Campbell and others ^{1984b} ~~1984a~~).

②

6.2.3 Outbreak Mode

Once an outbreak starts, declining survival among young larvae (probably primarily caused by competition for feeding sites during spring dispersal) appears to be important in maintaining the outbreak from one year to the next. During outbreaks, this survival rate appears to decrease as density increases (6.4.1). This phenomenon undoubtedly reduces the chance that later instars will exhaust the foliage and starve (6.4.5, 6.6.1).

②

6.2.4 Decline Phase

Outbreaks may decline through any combination of processes that can operate against dispersing small larvae, larger larvae, residual pupae, or adult moths.

Exceptionally low survival of the small larvae could be caused by differences in timing between larval emergence from hibernation and budburst (6.4.2), late frosts that destroy both the new foliage and the budworm, or foliage depletion through previous defoliations. Survival of the larger larvae is also at risk where most of the foliage has already been destroyed.

Parasitism among the residual pupae, which tends to be highest in places where mortality during earlier stages had already been high, may

accelerate the collapse of an outbreak (6.6.2). Adult moths are also likely to disperse to other sites with little foliage suitable for laying eggs.

①

6.3 Life Tables

Historically, forest managers have been most interested in forest pests after they reach high densities and threaten forest productivity or value (Mason 1978). Obtaining knowledge on how potentially damaging pest populations behave at sparse densities has been secondary. Currently, interest in the western budworm has shifted toward preventing possible future outbreaks through judicious management. To design appropriate preventive practices, managers need to know a great deal about both the processes that maintain populations at sparse densities, and the processes that upset this stability and lead to outbreaks.

Life tables represent an important tool for studies on population dynamics. One table can summarize much biologically rational information about a sequence of densities, mortality-causing factors, and fecundity in one place and budworm generation. Although life tables for forest insects go back at least as far as Tothill's work (1922), their usefulness was not recognized by many investigators until the classic paper by Morris and Miller (1954) on the development of life tables for the eastern budworm. Morris (1955) also described a pattern for developing sampling methods for the eastern budworm that has been adapted

by other workers. With these methods, investigators can estimate densities per unit of foliage area with specified confidence.

McKnight (1971) adapted Morris's methods to develop budworm life tables in Colorado. Carolin and Coulter (1972) also adapted these methods to develop sampling procedures for budworm in eastern Oregon. More recently, Waters and Volney adapted these methods for use in New Mexico and southwestern Oregon. Campbell and others (1983a) used or adapted these methods to develop life tables for budworm in the Pacific Northwest.

6-2A Successive average densities, derived from life-table studies, are shown in figure 6-2 for both the populations that increased and those that decreased. For almost every successive age interval, average survival was higher among populations that increased. Processes operating during each of these age intervals are discussed in following sections.

① 6.4 Early Survival

Among the Northwest populations studied between 1978 and 1982, survival from eggs to fourth instars (early survival) ranged from about 30 percent down to about 2 percent. Carolin (personal communication) estimated that survival from egg hatch to fourth instar was 43 percent in one plot, 7 percent in a second, and 6 percent in a third. Carolin later judged 6- to 7-percent survival to be more typical (Carolin, personal communication). Volney and Waters (1983 unpubl.) noted that survival at

this stage was high (37.1%) in a New Mexico population that increased 8.36 in a single generation. McKnight (1971) described average early survival of 64.9 percent for the populations he studied in Colorado between 1964 and 1966. The survival rates calculated by McKnight, however, use uncorrected estimates of density on midcrown branch tips. When these data were corrected to represent the whole plot, average early survival in these populations was estimated to be 18.8 percent (Srivastava and others, in press) $\frac{1}{M}$ within the range found by others.

② 6.4.1 Density Versus Early Survival

Egg densities ranged from about $\sqrt{3}$ to 1,000 eggs/~~per square meter~~ m^2 among the Northwest populations studied between 1978 and 1982. Across this range, almost no correlation was found between egg density and early survival ($r^2 = 0.08$).

Some populations studied recently in northern New Mexico (Stein and McDonnell 1982 unpubl.) were commonly much denser than any of the Northwest populations. Among these New Mexico populations, early survival declined from 5 percent in places and years where egg density was lowest to only about 0.1 percent where it was highest (fig. 6-3). Thus, early survival became a function of density above a threshold somewhere between $\sqrt{500}$ and 1,000 eggs/~~per square meter~~ m^2 . Other New Mexico populations studied by Volney and Waters (1983 unpubl.), which were either increasing or stable, within this density range showed a similar

correlation between density and early survival. Survivorship ranged from 41.1 to 1.0 percent in these populations, however. Some likely consequences of this relation are discussed in sections 6.4.5 and 6.6.1.

② 6.4.2 Egg Survival

The incubation period is brief; hatching occurs about 10 days after the eggs are laid (Carolin and Coulter 1972). During this interval, the eggs are in danger from parasites and predators and may fail to hatch from other causes.

Average hatch was 93 percent among populations studied recently in the Pacific Northwest. Parasitism was generally extremely low, averaging only 1.2 percent (Torgersen and others, in press). Average mortality from all other factors was 5.4 percent. Carolin (personal communication) also found high survival among eggs.

② 6.4.3 Fall Dispersal

Only a few estimates of fall dispersal have been made for western populations. After intensive study in two sites in north-central Washington, Eldridge and Egan (1983a unpubl.) found that survival during this interval was 39 percent in one site and 77 percent in the other.

④ Dispersal from the egg mass is initiated as soon as the larvae hatch. *Eastern budworm* larvae on silk threads can be carried long distances by the wind (Henson 1950), but the larvae generally hibernate within a few hours of hatch (Morris and others 1958a). During this brief interval, the larvae are at risk from spiders and other predators. Most of their mortality, however, can be attributed to dispersal.

of eastern budworm
Dispersal losses increase as the density of host trees decreases, and as the host stand becomes more isolated (Morris and Mott 1963). Miller (1958) characterized survival during this interval as more variable than survival among either eggs or larvae in hibernacula.

② 6.4.4 Hibernation Survival

Survival across this interval is both high and relatively invariant. In two populations in north-central Washington, Eldridge and Egan (1983a unpubl.) found survivals of 79 and 87 percent. Miller (1958) found remarkably similar survival (78 to 91 percent) in New Brunswick, and Terrell (1959) reported generally high and invariant survival in the northern U.S. Rocky Mountains.

② 6.4.5 Spring Dispersal

Most of the variability in survival during the spring appears to be a consequence of variable losses from dispersal. Multiple dispersal

episodes may be common, at least under some stand conditions. For example, Beckwith and Burnell (1982) found that dispersal of third and fourth instars represented about 38 percent of the larvae caught in dispersal traps in a mixed stand of Douglas-fir and western larch.

Spring dispersal begins as soon as the second instars emerge from hibernation. In northern New Brunswick, birds do not feed on young larvae of the eastern budworm (Cheshire 1959 unpubl.), but the larvae are again subject to predation by spiders and insects, as they are during fall dispersal (Mott 1963).

^a
↑
eastern budworm
Whether dispersing larvae live or die is largely a question of finding hospitable sites (Mott 1963). As in the fall, spring survival is directly related to the density of host trees and inversely to the degree of isolation of the host stand (Morris and Mott 1963). Western silvicultural recommendations are based partly on relations between the amount and placement of host foliage and the dispersal requirements of the larvae (Carlson and others 1983, Schmidt and others 1983, Wulf 1982 unpubl.).

In addition to problems with movement between hibernation site and suitable foliage, insects emerging from hibernation must also deal with possible asynchrony between their emergence and the availability of suitable food. Emergence of the population from hibernacula is prolonged, but most larvae hatch at about the same time (Volney and

others 1983^b). Thus, at least some larvae will find suitable feeding sites regardless of host phenology, but the rate of survival of the population depends on the degree of synchrony between budburst and the peak of second-instar emergence.

Losses during spring dispersal may reflect the probability that the larvae will find suitable food before their energy reserves are depleted. For example, an extended period of warm fall weather may critically deplete these reserves among ^{eastern budworm} the larvae that will have to find suitable feeding sites after they emerge from hibernation (McMorran 1973).

Recently, Thomson and others (1984) analyzed relations between budworm outbreaks and long-term weather in British Columbia. They concluded that outbreaks were triggered by warm, dry summers in conjunction with optimal timing between larval emergence and the flush of Douglas-fir buds. All five outbreaks recorded among the records analyzed by Thomson and his colleagues "were associated with warm dry summers in conjunction with synchrony of larval emergence and bud flush."

As reported before (6.4.1), early survival was inversely related to density, at least among dense populations in northern New Mexico. In all probability, this inverse relation reflects some sort of intraspecific competition among the larvae. Such competition seems most likely either in the fall ^I_M for places to hibernate ^I_M or during the following spring ^I_M for suitable needles and buds. If this inverse relation between density and

early survival proves generally true, it will probably also constitute a potent process in the population dynamics of the pest. Specifically, such a process would thin overly dense egg populations to densities that would minimize the chance of exhausting the host foliage and subsequent mass starvation. Such a process would tend to insure that ongoing outbreaks will persist.

① 6.5 Late Survival

② 6.5.1 Density Versus Late Survival

Fourth-instar densities ranged from about $\wedge$ (0.3 to 80 larvae/^{m²} per square meter) among the populations studied recently in the Northwest. Among these populations, survival from fourth instar to adult females (late survival) like early survival, ranged from about 30 percent down to 2 percent. Late survival was uniformly low among populations where density of fourth instars was below about three per square meter. Above this density, no clear relation appeared between density and survival.

② 6.5.2 Late Larval-Early Pupal Survival

Late survival is defined as survival from fourth instar to pupae

6-4A remaining after predation (residual pupae) (fig. 6-4). Late larval and early pupal survival ranged across about 15-fold, and they varied together ($r^2 = 0.85$). Similarly, Morris (1963)^a found a particularly

close correlation in populations of eastern budworm between survival during fourth through sixth instars and generation survival.

Much research has been devoted to events that occur during the late larval-early pupal interval. For this reason, description and discussion of the principal mortality-causing processes that operate during this interval are presented in a separate section (6.6).

②

6.5.3 Survival of Residual Pupae

Among the populations studied in the Pacific Northwest, survival of residual pupae ranged from about 25 to 100 percent. Except for two populations in north-central Washington, however, the lowest survival observed was about 50 percent. In general, survival of residual pupae was lower in north-central Washington than in the other areas.

Most of the variability in survival of residual pupae was induced by mortality from parasites (Campbell and others 1983a; Torgersen and others, in press). Among those populations, pupal parasitism ranged from a trace to 51 percent (Torgersen and others, in press). Parasites also appear to be a principal cause of mortality during this interval in other areas. For example, pupal parasitism accounted for 43 percent pupal mortality among the Colorado populations studied by McKnight (1971). See also table 6-1.

4 Variation in the survival of residual pupae played a generally minor role among western populations that have been intensively studied.

② 6.5.4 Proportion of Females

In 22 of 24 Pacific Northwest populations, the sex ratio among pupae was 1:1. In 21 of these populations, the sex ratio among adults was also 1:1. In all populations, differences between survival of male and female pupae were attributed to chance. The proportion of females among pupae did not differ on Douglas[^]-fir and grand fir, was slightly but significantly higher in the midcrown than in the lower crown, and was significantly higher in the one site studied where average defoliation of current-year shoots was greater than 50 percent (Campbell and others^{1984b}[^]).
~~1984b~~

Other investigators have also noted only minor departures from 1:1 in the adult sex ratio in populations of both eastern and western budworms. In New Brunswick, Miller (1963b) reported that the proportion of females ranged from 0.33 to 0.54. Miller concluded that "... this proportion did not differ markedly from the expected value of 0.50 during the outbreak, and changes that did occur had a negligible effect on generation survival and population trend." For these same data, Morris^a (1963)[^] found almost no correlation between the proportion of females and generation survival ($r^2 = 0.01$).

¶ In Colorado, McKnight (1971) found that 30 to 62 percent of the adults were female. McKnight thought that differential mortality among subadult males and females was probably because the males tend to pupate sooner, which would make them more susceptible to predation by both spruce coneworm larvae and female larvae of their own species.

In five of six sparse populations in southwestern Oregon (densities ranged from $\sqrt{0.87}$ to 12 eggs/~~per square meter~~^{m²} of foliage), the sex ratio was skewed in favor of males and the proportion of females was positively associated with density (Volney and Waters 1983 unpubl.).

Variation in the proportion of females among adults appears to have had a negligible effect on populations that have thus far been studied (but see also section 6.9).

① 6.6 Survival of Late Larvae and Early Pupae

② 6.6.1 Density Versus Survival of Late Larvae and Early Pupae

6-5A Survival of late larvae and early pupae is shown as a function of fourth-instar density in figure 6-5. Up to about $\sqrt{2.8}$ insects per square foot (30 insects per square/m²), these data show an inverse relation between density and late larval-early pupal survival. Above that density, the data are too sparse to discern any underlying relation.

¶ For western budworm, our highest recorded densities were 160 fourth instars per square meter. For eastern budworm, Watt (1963) showed that late larval survival continued to increase slightly to about 140 fourth instars per square meter. Ultimately, as densities increased beyond that point, average survival decreased.

Obviously, fourth[^]-instar density commonly exceeds 80 per square meter among populations of the eastern budworm. Conversely, fourth[^]-instar densities of western budworm greater than about ^{9.3 per square foot} 100 ^{m²} per square meter were rarely found in either the Pacific Northwest or in northern New Mexico by either Stein and McDonnell (1982 unpubl.) or Volney and Waters (1983 unpubl.).

As described earlier (6.4.5), the apparent upper limit on fourth[^]-instar densities in the northern New Mexico populations was induced by an inverse relation between egg density and early survival (fig. 6-3). No similar relation has been suggested for the eastern budworm. If this major apparent difference between the numerical behavior of the two budworm species proves to be general, it should provide much of the basis for understanding both the relatively indeterminate duration of outbreaks by the western species and the relatively mild biological effects of those outbreaks, compared to the eastern budworm.

②

6.6.2 Role of Parasites

The bulk of our information about natural enemies of both the eastern and western budworms has been obtained during outbreaks, and to some extent during the decline phase of these outbreaks. Varty (1974) indicated that about 150 species of arthropods attack the budworms, and that about a third of these are predators.

Fourteen species of parasites were consistently represented in rearings from populations of the budworm studied recently in the Northwest. Torgersen and others (in press) listed the species as follows, in approximate order of decreasing dominance:

Apanteles fumiferanae Viereck, Glypta fumiferanae (Viereck), Charmon gracile (Provancher), Enytus montanus (Ashmead), and Mesochorus tachypus Holmgren¹—a secondary parasite; all from larvae. Species reared from pupae were: Agria housei Shewell, Madremyia saundersii (Williston), Ceromasia auricaudata Townsend, Phaeogenes maculicornis hariolus (Cresson), Itoplectis quadricingulata (Provancher), Ephialtes ontario (Cresson), Phorocera incrassata Smith, and Timavia fumiferanae (Tothill). Trichogramma minutum (Riley) was the only parasite reared from budworm eggs.

The percentage contribution of parasitism to total killing power (equivalent to the killing power defined by Varley and Gradwell 1960) was lowest among the populations in Idaho and Oregon, intermediate in Montana, and highest in Washington (table 6-1). Because the contribution of parasites was highest in Washington where the populations had been decreasing for several years, parasites may be reinforcing the decline of these populations (Torgersen and others, in press).

Several investigators have concluded that parasites play a substantial part in regulation of eastern budworm at sparse densities, but that their potential for rapid numerical response can not curtail host numbers once release has begun (Blais 1960, Dowden and others 1948, Graham and Orr 1940, Miller 1963b, Tothill 1923). Morris and others (1958a) believed that the pronounced delay in response of parasites was compounded by adult-dispersal behavior of the eastern budworm, which could dilute or destroy developing synchronization between the budworm population and its parasite complex. This same observation could also apply to other natural enemies. Apparent increases in parasitism during a decline of the budworm could simply indicate that the residual population, which has already suffered heavy losses, is immediately subject to pressure from a parasite complex that is still increasing in response to the former density of the host.

② 6.6.3 Role of Birds and Ants

At the start of the CANUSA program, information about the role of birds in the West was limited to a record attributing the collapse of an outbreak at Lillooet, British Columbia, to the joint effects of birds and parasites (Wilkes 1946). In contrast, a wealth of information was available on the role of birds in the dynamics of budworm populations in the East. They had been identified as playing significant roles in terminating outbreaks of the eastern budworm (Blais and Parks 1964, Dowden and others 1950, Jaynes and Drooz 1952). Dowden and others (1948, 1953) found that about 15 species of resident and nonresident birds fed heavily on the eastern budworm. Shooting-out techniques by Dowden and others (1953) and caging studies by Jaynes and Drooz (1952) demonstrated striking quantitative effects of excluding birds (and parasites) from individual trees and entire plots.

Detailed studies on avian predation on the eastern budworm (Mook 1963, Morris and others 1958a) indicate that predation was greatest during the sixth-instar and pupal stages. All bird species, particularly three warblers, showed pronounced, direct numerical responses to budworm density. Graham and Orr (1940) suggested that the scarcity of insectivorous birds brought on by a combination of unfavorable weather and lack of food may have stimulated an eastern budworm outbreak in Minnesota. Most recently, Crawford and others (1983) concluded that birds ate about 87, 23, and 2 percent of the insects in sparse, transition, and dense populations of the eastern budworm.

In 1979, several species of birds were commonly observed preying on the western budworm. Two sites, with single-branch bird exclosures (Campbell and others 1981) had pupal densities on protected branches twice as high as on control branches (Torgersen and Campbell 1982). These studies stimulated studies on insectivorous birds (see section 6.4).

Ants were also seen investigating and eating the budworm. In 1980, to cite an extreme example, 96 separate observations were made of ants investigating or eating pupae in 48 hours after 150 pupae were stocked in one site in north-central Washington (Campbell and Torgersen 1982). Between 1979 and 1982, species of ants observed eating budworm pupae include the following: Camponotus modoc Wheeler, C. vicinus Mayr, C. laevigatus (Smith), Formica haemorrhoidalis Emery, F. accreta Francoeur, F. podzolica Francoeur, F. neorufibarbis Emery, and F. lasiodes Emery (Youngs and Campbell 1983 unpubl.).

Ant predation on both the eastern and western budworms has been observed by other investigators. Mathers (1932) in British Columbia and Thomson (1957) in Ontario considered ants important budworm predators, and both Bain (1974) and Markin (1979^{unpubl.}) identified ants as predators of the western species.

In 1980, whole-tree exclosures and sticky barriers were used to exclude avian predators, predaceous ants, or both from (9 ~~ant~~ ^{out-tall (9-m)}) (29.5 ~~ft~~ ^{ft}) open-grown trees on one site in north-central Washington and four sites

in central Idaho. Budworm on these trees were protected from about the fourth instar until they either died or became adults. At the lowest budworm density (1.7 fourth instars per square meter), 10 to 15 times as many adult moths were produced on trees protected from both birds and ants as on control trees. Even when fourth-instar density was $\frac{2.3 \text{ insects}}{1 \text{ m}^2}$ ^{insects per square meter}, ~~25/1000 m²~~ ^{per square meter} adult density continued to be about twice as high on protected trees as on controls. Birds alone or ants alone were usually sufficient to greatly dampen the high survival observed when both groups were excluded (fig. 6-6).

In 1981, the trials initiated in 1980 with whole-tree exclosures and sticky barriers were continued on sites in northwestern Montana and eastern Oregon. Again, the results showed a strong inverse relation between budworm density and the effects of birds and ants. This predation, combined with mortality from all other sources, was consistently adequate to reduce survival across the late larvae to early pupal interval to about 5 percent in populations with fourth-instar density less than one insect per square meter. When these predators were removed, however, average survival increased to about 40 percent (fig. 6-7). Unless other processes upset low-density stability, predation by birds and ants can maintain most budworm populations in the Pacific Northwest at sparse densities indefinitely.

The relative influence of birds versus ants can be greatly influenced by stand age and structure. For example, birds were as effective in

destroying pupae on branches in the upper crowns of tall trees as on branches at about breast height; ants, however, were only effective on low branches (Campbell and Torgersen 1983^b). In contrast to the dominance of birds on tall trees, the roles of birds and ants tend to be reversed on seedlings (Campbell and others^{1984a} ~~1983~~).

② 6.6.4 Habitat Requirements of Avian Predators

Edward O. Garton

Dramatic increases in budworm populations on trees protected from forest birds (fig. 6-6) has heightened interest in them, their habitat requirements, and potential for managing their populations (Takekawa and others 1982). Ecological characteristics of bird species occurring in western forests have been summarized in detail for only two regions (Thomas 1979, Verner and Boss 1980). Potential approaches to managing many of these species were examined in a series of symposia (Smith 1975, DeGraff 1978, 1980). Bird species known to consume western budworm can be grouped into guilds based on their feeding activities during the spring and summer. The major ones are: flocking, conifer gleaning, shrub gleaning, ground foraging, and flycatching. The birds within each guild show many similarities in feeding behavior, diet, nesting requirements, and taxonomy. The role of the species known to be important in regulating budworm populations and their habitat requirements are summarized, by guild, in this section.

③ 6.6.4.1 Flocking Guild¹ In spite of their general classification by ornithologists as seed-eaters (Bent 1968), the members of the flocking guild show the highest rates of consumption of budworm larvae and pupae (table 6-2). These species are unique in the forest bird community in that they are not territorial during the breeding season, but forage widely in flocks (Bent 1968). Because of this, their numbers may increase enormously on sites experiencing budworm outbreaks. These species all nest in conifers or deciduous trees (table 6-2);

T6-2
consequently, they breed more commonly in mature and old-growth stands than in early successional stages (table 6-3). Their occurrence in a particular stand is sporadic from year to year and most likely related to insect abundance. The flocks appear to be nomadic during the nonbreeding period, moving from area to area or even region to region in search of seeds of conifers and other trees (Bent 1968). During the late summer and fall, they consume large quantities of berries. Beyond these general statements, little is known about the specific factors influencing the numbers of these species from year to year and stand to stand.

③ 6.6.4.2 Conifer-Gleaning Guild¹ Budworm consumption by the large guild of conifer gleaners (table 6-3) ranges from two to over six budworm larvae and pupae per bird per hour (table 6-2). These species are all strongly territorial, with consequent stability in numbers from year to year in any particular stand. They hunt for insects on the foliage and small branches of conifers during the breeding season and play a major role in maintaining sparse budworm populations during intervals between

outbreaks. The species resident in fir and mixed-conifer forests during the winter $\frac{1}{M}$ such as chickadees and kinglets $\frac{1}{M}$ probably consume large numbers of hibernating larvae. The species in this guild are most diverse in mature and old-growth forests, and the total number of birds in this guild increases with increasing volume of foliage (MacArthur 1958, Garton and Langelier, in press). The guild is most abundant in stands with a multistoried canopy and an abundance of shrubs (Garton and Langelier, in press). The habitat requirements of many of these species are well studied (Bent 1963b, 1964a, 1964b, 1964c, 1965a, 1965b, 1968). Some, such as the yellow-rumped warbler and the western tanager, are adaptable and occur widely. Others $\frac{1}{M}$ such as the chickadees $\frac{1}{M}$ have specific nesting requirements, which may limit where they occur (Thomas 1979).

③ 6.6.4.3 Shrub-Gleaning Guild $\frac{1}{M}$ Members of the shrub-gleaning guild feed in shrubs predominantly and conifers secondarily. Mean consumption rates varied from 1.7 to 6.0 budworm per bird per hour (table 6-2). These species nest in or under shrubs and are less abundant where shrubs are reduced (Garton and Langelier, in press).

③ 6.6.4.4 Ground-Foraging Guild $\frac{1}{M}$ Members of the ground-foraging guild feed on the ground and in the grasses, forbs, shrubs, and lower foliage of trees. Mean budworm consumption varies from 1 to 15 larvae and pupae per bird per hour (table 6-2). These species are territorial and do not show major increases in abundance associated with budworm outbreaks. They

apparently shift their foraging locations from the ground and low vegetation to the lower portion of the canopy during outbreaks and apply additional pressure toward suppression of outbreaks during the period of initial buildup. Several of these species nest in shrubs, and most depend on the low vegetation in some way. Even those species nesting on the ground require low vegetation to cover the nest. Members of this guild occur in all successional stages and are particularly associated with ecotones (table 6-3).

③ 6.6.4.5 Flycatching Guild¹—Only the Hammond's flycatcher in the flycatching guild consumes many budworm larvae and pupae (table 6-2), but the members of this group probably consume many adults. This guild is most abundant in later successional stages (table 6-3) and in diverse stands with an open canopy structure (Bent 1963a).

③ 6.6.4.6 Other Guilds¹—Some of the other groups of birds occupying forest stands, such as the raptors, are unlikely to play a direct role in budworm population dynamics. Such groups as woodpeckers, however, which feed extensively on tree trunks during winter, and swifts and swallows, which consume large numbers of adult lepidopterans in the air, may be valuable budworm predators. Members of other guilds have been observed to feed on moths. The roles of these groups relative to budworm have not been studied.

② 6.6.5 Other Mortality-Causing Factors

Robert W. Campbell

Casual observations have shown that insectivorous mammals eat both late instars and pupae. No attempt has been made, however, to quantify the effect of this predation. In the East, Morris (1955) noted that most of the large larvae that drop to the understory are eaten by white-footed mice, Peromyscus leucopus Rafinesque. As an influence on eastern budworm population dynamics, however, small mammals have essentially no effect (Morris and others 1958a).

The activity of arthropod predators is seldom reported. Brief mention is made of predation by representatives of several groups, such as a clerid beetle and a snake fly (Carolin 1974), a carabid beetle (Sanders and Frankenhuyzen 1979), and mites (Jaynes and Drooz 1952). But most of the interest in arthropod predators of the budworms has been in spiders (Loughton and others 1963, Turnbull 1956). These authors concluded that spiders take whatever prey is most abundant, and that by sheer weight of numbers they are important in budworm regulation. The web-spinning therediids and the hunting salticids constitute the dominant families known to prey on budworm.

Four groups of microorganisms¹_M microsporidia, viruses, bacteria, and fungi¹_M are known to occur in all budworm stages except the egg. The relevant literature was reviewed by Neilson (1963), who concluded that

the diseases affecting the eastern budworm are only mildly infectious and have low epidemiological potential. In populations studied in the Pacific Northwest between 1978 and 1982, only a very few specimens showed symptoms of lethal infectious or noninfectious disease.

At least across the interval from fourth instar to adults, survival of populations in the Northwest consistently approached a high constant on trees that had been protected from birds and ants (figs. 6-6, 6-7). Increased mortality from other sources did not effectively compensate for their absence. In short, other, mortality-causing factors played a minor role in regulating late survival, once birds and ants had been excluded (Campbell and Torgersen 1983^a).

② 6.6.6 Foliage Quality

Recently, several investigators have examined relations between the natural defensive chemistry of Douglas-fir and success of the western budworm. To explore some of the reasons why populations rarely reach outbreak densities west of the Cascade Range, Perry and Pitman (1983) tested responses of larvae to foliage from seedlings of both west-side Douglas-fir (var. menziesii) and interior Douglas-fir (var. glauca) grown in the same west-side garden. Surprisingly, foliage from the interior Douglas-fir caused a wide range of larval mortality; foliage from the west-side Douglas-fir caused no significant larval mortality. Perry and Pitman concluded that environmental factors east of the Cascades may

alter the ability of the trees to produce allelochemicals, and thus play a key role in regulating interior populations. They concluded that the apparent lack of defensive chemicals in west-side Douglas-fir suggests either that "inducible defenses may play a role" or that predators and parasites may keep budworm populations at low densities in west-side ecosystems.

1983a, 1983b

Studies by Cates and others (~~in press~~) indicate that the terpene complement associated with resistant trees in Montana was different from that found in New Mexico. From agar-diet studies, they found that high concentrations of bornyl acetate and beta-pinene—similar to the concentrations found in the foliage of resistant trees—increased the duration of the larval stage and decreased dry-weight production of the larvae. [Available foliar nitrogen did not appear to be important, but trees that flushed relatively late in the season harbored fewer larvae and sustained less defoliation.]

① 6.7 Observed Eggs Per Female

In the Pacific Northwest, the number of eggs deposited per female pupal case (observed eggs per female), ranged across about 100-fold, from a low of about 10 to a high of about 1,000. The correlation between observed eggs per female and annual trend is $r^2 = 0.25$. As suggested earlier (Campbell and others 1983a), both the range in the number of eggs deposited per female and the correlation between this number and annual

trend show that variation in observed eggs per female has an important influence on the dynamics of this life system.

Although many complex processes are involved (Greenbank and others 1980), observed eggs per female moth is the result of both the average fecundity of those moths at the time they emerge, and the net result of all the processes of migration and mortality that influence those moths until they die or finish laying their eggs.

② 6.7.1 Fecundity

In any population, average fecundity can be estimated by rearing a sample of mated female moths and counting the eggs they produce. Fecundity is affected largely by the quantity and quality of food available to the preceding larvae (Blais 1952, Kirkbride and Wagner 1983^a unpubl., Miller 1963a). Other extrinsic factors that may affect fecundity indirectly include weather (Greenbank 1956), the availability of suitable places to lay eggs, and disease (Neilson 1963). In populations of both eastern and western budworms, mean fecundity is closely correlated with size or weight of female pupae (Kirkbride and Wagner 1983^a unpubl., Miller 1957).

Average fecundities ranged from about 100 to 200 among populations studied in the Pacific Northwest. Almost no correlation was found between these fecundities and the observed number of eggs per female pupal case ($r^2 = 0.03$). Apparently, variation in average fecundity had almost no effect on the number of eggs actually deposited per female moth.

② 6.7.2 Index of Adult Dispersal

The net results of moth migration and mortality (index of adult dispersal) can be estimated from the ratio between egg density on the foliage and the innate egg-laying ability of the emerging females.

Relations between the index of adult dispersal and observed eggs per female pupal case (fig. 6-8) are very close ($r^2 = 0.92$). Thus, almost all of the variation in observed eggs per female pupal case resulted from variation in adult migration and mortality. Immigration clearly exceeded the combined effects of emigration and mortality where observed eggs per female pupal case were greater than the inherent ability of females to produce eggs (about 200). Significantly, observed eggs per female pupal case were consistently much greater than 200 among the populations we studied in eastern Oregon at the start of the current outbreak. Just as in eastern budworm, redistribution of adult female moths appears to be a major factor in the population dynamics of the western species (Campbell and others^{1984b}).

② 6.7.3 Density of Adult Females Versus Egg Density

Redistribution of adult females clearly seems to be a major factor in western budworm population dynamics. In 1981, the life-table studies were supplemented with data from ten additional sites: six in southwestern Montana and four in eastern Oregon. Both adult female densities and subsequent egg densities per square meter were estimated on each of these additional sites.

4 Egg density in the 46 Northwest populations was examined as a function of both the density of preceding adult females and an index of defoliation. This index, based on average defoliation of current-year shoots, was:

No defoliation = 1;

0 < defoliation $\leq$ 25 percent = 2;

25 percent < defoliation $\leq$ 50 percent = 3; and

50 percent < defoliation $\leq$ 75 percent = 4.

Average defoliation of current-year shoots never exceeded 75 percent among the populations studied.

6-9A Relations between adult females, defoliation, and subsequent egg density are shown in figure 6-9. Only 15 of the 46 predicted values (33 percent) were within ± 20 percent of their observed values. Seventeen predicted values (36 percent) deviated from observed by more than ± 75 percent.

Perhaps much of the variation in the density of eggs not associated with either the density of adult females or defoliation will prove to be a function of identifiable characteristics of sites and stands. Only further studies can provide an answer.

Appendix VIII



4100 Timber Management Research

Date February 16, 1983

Subject: Analysis of Garton's Data For Bob Campbell

To: Nick Crookston

This memo describes the procedure taken to process the tree and stand data provided by Oz Garton to conform to Bob Campbell's analysis needs.

PROCEDURE

STEP 1:

The two data sets provided by Lisa Langelier were copied from tape to disk.

The first data set TREES consisted of a SAS data library divided into the four states IDAHO, WASHINGTON, MONTANA, and OREGON. Each of these members contained the tree records for all of the sites in each respective state. The information coded on each tree record was SITE, TRANSECT, SEGMENT, BOLE HEIGHT, DIAMETER, CROWN RATIO, HEIGHT, RADIUS, and SPECIES. The entire TREES data set had 20,847 observations.

The second data set STANDS consisted of 572 observations that had the following information: PLOT NUMBER and STAND. This data set identified the stands in each site indirectly by PLOT NUMBER. The PLOT NUMBER was calculated from the following equation:

$$\text{PLOT NUMBER} = \text{SITE} * 1000 + \text{TRANSECT} * 100 + \text{SEGMENT}$$

STEP 2:

A) A data set STANDINFO was created that contained the following information used by the STAND PROGNOSIS MODEL for each stand: ELEVATION, ASPECT, STAND, HABITAT TYPE, AND SLOPE.

B) Another data set BUGPLOT was created and contained the following data elements: PLOT NUMBER and BUG. The BUG variable denoted if a particular PLOT NUMBER in a site was a bug plot. Differentiating which plots were bug plots was accomplished by examining the site maps and then calculating the plot numbers that were included in each bug plot.

STEP 3:

A) A merge was executed between the data sets STANDS and STANDINFO with the merge key being STAND. This associated the stand information required by the model with the plot numbers of the stands. This created data set STANDALL which had the following data elements: STAND, PLOT NUMBER, ELEVATION, ASPECT, HABITAT TYPE, SLOPE, and 572 observations.



B) A merge was executed between the two data sets STANDALL and BUG PLOT with the merge key being PLOT NUMBER. This new data set, also named STANDALL, held all of the information needed to process the sites. STANDALL consisted of the following elements: STAND, PLOT NUMBER, ELEVATION, ASPECT, HABITAT TYPE, SLOPE and BUG.

STEP 4:

A) A SAS program was written and executed that created the variable PLOT NUMBER given by the above equation from the information contained on the TREES data set tree records. This new variable was appended onto each of the tree records in data set TREES.

B) A sort was executed on the TREES data set that sorted it by PLOT NUMBER.

C) A sort was executed on the STANDALL data set that also sorted it by PLOT NUMBER.

STEP 5:

A) A SAS program was written that merged the TREES and STANDALL data sets together with the PLOT NUMBER as the merge key: At this point all the information needed by the STAND PROGNOSIS MODEL was available. This new data set was called TREESALL. TREESALL contained the following information: DIAMETER, HEIGHT, BOLE HEIGHT, CROWN RATIO, RADIUS, SPECIES, SITE, TRANSECT, SEGMENT, PLOT NUMBER, ELEVATION, SLOPE, ASPECT, STAND, BUG and HABITAT TYPE.

B) A SAS program was written that created a new data set, OZALL, that 1) dropped the variables from TREESALL not needed by the model 2) dropped tree records that had a diameter of greater than 88 inches 3) sorted this data set first by site, then by stand 4) converted the new data set from a SAS data set to an OS data set 5) omitted tree records with non-valid plot numbers. BOLE HEIGHT, RADIUS, SEGMENT and TRANSECT were dropped when OZALL was created. The OZALL data set had the following elements in the columns indicated: SITE 1-3 PLOT NUMBER 5-10 STAND 12-15 ELEVATION 17-20 ASPECT 23-24 HABITAT TYPE 26-29 SLOPE 31-32 BUG 34-35 DIAMETER 37-40 HEIGHT 42-45 CROWN RATIO 48 SPECIES 37-40.

STEP 6:

A Fortran program was written that created prognosis keyword files. This program put only those tree records in each site that were included in the bug plots. Some sites had no bug plots so they were not included. This program also edited data from the tree records, i.e., 1" dbh trees 70 meters tall, trees with dbh's 88 inches etc.

STEP 7:

The prognosis runs were made.



United States
Department of
Agriculture

Forest
Service

CANADA/UNITED STATES SPRUCE BUDWORMS PROGRAM-WEST
Pacific Northwest Forest and Range Experiment Station
P.O. Box 3890
Portland, Oregon 97208

Final

Re: 4040 Cooperation

Date: October 13, 1983

Subject: Cooperation with CANUSA-West Modeling Effort

To: R. W. Campbell
Nilima Srivastava

Ron Stark's April 25, 1983 memo to Bob outlined five items that Ron perceived to be Bob's responsibility for the remainder of FY 1983. At Bob's request, a May 5, 1983 memo from Ron to Bob elaborated on the information requested as part of Item 5. This description indicated that Colbert, Sheehan, Crookston, and Kemp were interested in information regarding the effects of site and stand condition^s of budworm densities or survival among crown levels within a stand or among stands.

Nilima's August 29, 1983 memo to me included models (summarized in matrix form) that relate certain site and stand characteristics to within-stand budworm densities and survival rates. Between-stand densities or survival rates were not mentioned. Frankly, I expected more than just one page of formulae with no definition of the terms used. I sent a memo to Nilima requesting some additional information, expecting that it would take an hour or two to answer my questions.

Bob responded with a memo to me (15 September, 1983) asking that I "rethink [my] need for the additional detail [I] requested". Kathy Sheehan and I met with Bob on September 23 to discuss the issue, and we offered to explain, question by question, why each question had been asked. Bob stated that he preferred a written statement from us. So here goes.

1. How many plots and years and how many trees in each plot were included in the data base used to develop your models?

Sheehan has compiled a list of plots and years where you conducted budworm population studies (April 25 memo from Ron to Bob). However, I am not certain that site and stand information was collected at all these locations. Also, I do not know if data collected in 1983 was included in the analyses. Knowledge of the number of sites studied and the number of budworm population observations at each site greatly enhances my ability to evaluate whether additional research is warranted.

My question regarding the number of trees sampled per plot arose due to additional questions about how site and stand conditions were measured on your plots. I was concerned that in the open-grown areas (where you generally worked), very few trees might fall into a given variable radius plot; if only a few such plots were measured in each area, the actual site and stand conditions may not be well represented by your subsample. I would therefore appreciate a brief description of the sampling design that was used: Were all trees on the 5 ha plots (used in your budworm population studies) censused, or



were subsamples taken? If subsampled, how many "points" were sampled per plot, and what methods were used? If a fixed plot was used, what was its area? If a variable radius plot was used, what basal area factor was used?

2. What sizes of trees were included in the data base? What species of hosts were included? Could analyses be done on one or more hosts separately?

I know that you generally sampled budworms on "average-sized" trees (7-14m), though some work was done on larger and smaller trees. Did the budworm population data used to develop Nilima's models come only from average-sized trees, or is some data from larger and/or smaller trees included? Since the Budworm Model is designed to allow different survival rates and densities on different tree height classes, it would be useful to know what sizes of trees were included in your analyses.

I also know that you sampled budworms on Douglas-fir and grand fir, and that in some previous analyses you have pooled observations from these hosts. Were budworm samples from Douglas-fir and grand fir pooled in this case? Did you try to develop separate models for each host? Again, this knowledge helps me evaluate what was done and judge whether additional research is justified.

3. Please define these variables as used in your models:

Percent Host (% of total stems? volume? basal area?)

Avg. Dominance (is this average height of dominant trees?)

Live Crown Height (is this live crown length? live crown ratio?)

Avg. Height (of all trees? or just dominants?)

Several plausible definitions exist for many of the variables used in Nilima's models. Some variables, such as "Avg. Dominance" and "Live Crown Height", are truly puzzling to me and are not standard Prognosis Model output. Obviously, a clear understanding of the variables used is essential for evaluation of your analyses.

4. Please list all the variables that were considered in your analyses. For example, habitat type is not a parameter for any of your models; did habitat type not contribute significantly to any model, or was it not tested?

I hope this question is self explanatory. Knowledge of which variables were tested for inclusion in Nilima's models helps me evaluate the completeness of your analyses.

6. Were there any significant interactions among model parameters? For example, did budworm density or survival on a particular host vary according to habitat type?

The models that Nilima provided included no interactions. Regarding the example given, field observations of several experienced foresters and entomologists have suggested that on Douglas-fir and grand fir, budworm generally "does better" in some habitat types than others. From the limited information accompanying Nilima's models, however, I don't know if a) you tested for this type of interaction and found no evidence, or b) you did not consider interactions. Again, this knowledge would help me evaluate your analyses.

Were multivariate techniques the only analytic methods considered? Why?

Knowing what methods were attempted and why will allow us to make suggestions for further work.

8. What was the significance of the various models?

Though you stated that the significance was poor (p .3), you did not specify the significance of specific models. I would like to know if some models showed more "promise" than others. Such evidence may assist me in recommending future research directions.

9. Could you provide some further information on distribution or survival rates by some other stratification?

We had suggested that you examine within-stand budworm densities and survival rates as stratified by crown thirds. I thought that as you worked with the data, other possible stratifications (dominant-codominant vs. intermediate-suppressed trees, for example) might occur to you. This question was intended to offer you an opportunity to suggest other possible approaches to these analyses.

10. Can you provide a summary of what data is available for eggs to larvae? You state that there is almost no data sufficient for analysis of stratum-specific survival rates. Mean, variances, and sample sizes by plot, year, and host species will be useful.

This question concerned both budworm and site and stand data: What habitat types were sampled? What was the mean, variance, and range observed in basal areas? in budworm survival? I can't determine whether additional research is justified without knowing what range of conditions have already been examined.

Let me know if you still have questions or concerns about these questions.

I was surprised to hear Bob say that you spent an entire day drafting your September 15th memo. If reasonable documentation of the analyses had been kept, you should have been able to answer these questions in just a few hours. That would have saved us your day drafting a response, our meeting time on September 23, and my efforts in drafting this memo.

Please provide me with the requested information by October ²⁵~~24~~, 1983.


J. J. COLBERT
Research Coordinator

cc: Sheehan ✓
Stark
Wickman



4040 Cooperation

Date: November 17, 1983

Subject: Larval Instar Distribution

To: J. J. Colbert/K. Sheehan
CANUSA-W, Portland

The following is in response to your letter of 6 June regarding the information we supplied in our letter of 25 May.

The listing of percentage larval instar composition by site and date are based on the following assumed means and ranges: $L_{III} \bar{x} = 0.46 \pm \text{ca. } .08 \text{ mm}$;

$L_{IV} \bar{x} = 0.73 \pm \text{ca. } 0.12$; $L_V \bar{x} = 1.21 \pm \text{ca. } 0.21$; $L_{VI} \bar{x} = 1.90 \pm \text{ca. } 0.48$.
These are based on our work to date, and on published literature as given in our letter of 25 May.

Plot Location	Date(s)	Percent			
		L_{IV}	L_V	L_{VI}	N
Camp Utmost, MT	VI-29-82	71.4	28.6	0.0	297
Arkansas Cr., MT	VI-30-82	23.1	52.3	24.6	130
Kozy Corners, MT	VII-1-82	39.1	56.6	4.3	297
Cove, OR	VI-29-30-82	42.4	55.9	1.7	59
Starkey, OR	VII-2-82	12.6	49.0	38.5	349
Raven, OR	VI-26-27-82	1.8	33.7	64.5	169
Frazier, OR	VI-27-28-82	3.9	36.5	59.6	364
Camp Utmost, MT	VII-7-11-81	14.8	30.0	55.2	1597
Archibald Loop, MT	VII-16-81	0.0	45.5	54.5	11
Arkansas Cr., MT	VII-11-12-81	26.6	37.5	35.9	66
Kozy Corners, MT	VII-13-14-81	2.4	12.0	85.6	1181
Raven, OR	VI-21-27-81	49.2	47.5	3.3	120
Frazier, OR	VI-21-27-81	35.5	61.9	1.6	63
Lardo, ID	VII-7-9-81	17.7	10.4	72.0	328
Red Ridge, ID	VII-1-16-81	13.8	13.2	73.0	600
Red Ridge, ID	VI-27-30-80	29.5	67.6	2.9	139

At this point, our analyses of the reliability of using pigmentation patterns to assess larval instar distribution are still incomplete. A confounding factor is the possibility that some populations may have significant proportions of larvae with seven instars.

Torgy
TOROLF R. TORGENSEN
Research Entomologist



SP
11/27/83

File
Campbell/Torgensen
FY83



Reply to:

1530 Interdepartmental

Date:

October 18, 1983

Subject:

Cooperation with Canusa-West Modeling Effort

To:

J. J. Colbert

Here is the information you requested in your memo of October 13, 1983:

1. The number of trees per plot sampled to get the population data for each life stage was specified in our three sampling papers--one for egg masses, one for L-4, and one for pupae. You have had a copy of each of these papers for about a year now. The site and stand information we used was provided by Nick Crookston from data collected by Oz Garton's crew. Nick would be a good person to talk to about tree selection to run Prognosis. Since you are working so closely with the stand prognosis model, you cannot possibly have a worse idea of what variables 1-12 mean than I do. Any other details that you need could best be provided by either Oz Garton's group or Nick Crookston. The 1983 data were still being collected when these analyses were performed. There was no way of including them in analyses done before September 30.
2. As you can see from the attached sheet, we had only 14 plots where both population estimates and site and stand descriptors were available. This is hardly a reasonable data base, given the range of conditions that exist in the western conifers. As you already know (from all the population estimates for all our plots given to Kathy Sheehan in April) we sampled all size trees for only the egg-mass stage. Further, these samples were only taken from 5 of the 14 plots on the attached sheet. There is no way we could have included different size trees in our analyses.

Again, only 4 of the 14 plots had information on both Douglas-fir and grand fir trees, which did not allow for analyses by host species.

3. I am just as much puzzled by the variables as you are. They were provided by Nick Crookston and I took them to be standard. Please ask him about the variables, since they are his creation.
- 4&6. The variables are listed in the attached sheet. All variables (1-12) were entered as linear variables with 12 variables and 15 data points, there aren't any degrees of freedom left to consider interactions.
5. Omitted in your memo.

CANUSA ROUTING:	✓	INITIALS
Prgm Manager		
Secretary		
Res. Coord.	✓	JJC 10/24/83
Appl. Coord.		
Modeler	✓	KS 10/24
Editor		
Other		



7. The distribution of budworm in any given crown third is highly correlated with the distribution of budworm in other crown thirds ($r^2 > .78$). Since the dependent variables (insects in each crown third) are highly correlated, the only analyses that can be used are multivariate. Use of univariate techniques would violate basic assumptions.
8. When I say min. $p > .3$, it means that the model that showed the most promise had a significance level of 0.3.
9. With a limited data base ($n = 14$), its not possible to do much. One needs a much larger base of site and stand conditions.
10. The means, variances, and sample sizes, by plot, by year, and by host species provided to Kathy Sheehan in April will give you the information you request here.

Note: Sometimes we had two sets of densities for any given place, which gave us $n > 14$.

Nilima Srivastava

Nilima Srivastava

Enclosure

cc:
Wickman

Site	1	2	3	4	5	6	8	9	10	11	12	13	
New. M.	--	0	--	75	43	16	199	66	61	62	7.8	260	✓
Red. R.	4	0	52	65	69	78	92	35	32	39	8.4	520	✓
Pond.	3	2	52	75	75	66	180	83	81	102	9.2	310	
Lardo	6	0	51	60	66	69	180	67	72	50	8.3	520	
BS Place	6	0	40	75	36	68	273	86	91	101	7.6	310	
Tw. Rv.	6	1	32	85	89	85	497	153	150	117	7.5	310	
Rat. Cr.	9	0	28	85	85	79	347	221	208	109	10.8	310	
Rob. Cr.	5	2	26	25	82	75	809	271	134	250	7.8	310	
Utmost	5	2	45	75	59	77	165	55	51	64	7.8	310	*
Arch.	9	0	41	35	43	14	388	58	59	52	5.3	250	*
Ark. Cr.	9	2	40	85	56	51	156	55	52	57	8.1	310	
Kozy K.	5	2	44	65	36	57	273	67	65	45	6.7	310	*
Raven	7	1	48	55	66	73	229	77	86	51	7.8	310	*
Frazier	2	1	47	62	26	58	148	81	74	61	10.0	310	*

<u>Variables #</u>	<u>Description</u>
1	Aspect
2	Slope
3	Elevation
4	Live Crown Height
5	Average Height
6	Percent Host
7	Trees per acre
8	Basal area/acre
9	CCF
10	Avg. dominance
11	DBH, quadratic mean
12	Habitat type
13	* All size trees sampled
	✓ Two host species sampled

Note: These variables are summary variables generated by Nick Crookston using stand Prognosis model. Oz Garton's crew sampled for the initial variable that went into stand prognosis.